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BULLETIN
OF THE
TORREY BOTANICAL CLUB

VOLUME 66 JUNE · 1939 NUMBER 6

The Genus Pholistoma Lilja[1]

LINCOLN CONSTANCE

(WITH ONE FIGURE AND PLATE 7)

The three species and one variety included in this paper have been segregated from *Nemophila* Nutt. and *Ellisia* L., respectively, because they are thought to constitute a natural group quite distinct from either of these two genera. The customary disposition of two of the species within *Nemophila* with plants radically unlike themselves, was based upon the assumption that the possession of intersepaloid bracts on the calyx was, in itself, a condition forming a trustworthy generic boundary to distinguish distinct and natural species-assemblages. Into *Ellisia*, on the other hand, was placed the third species, chiefly because it lacked the characteristic auricles of *Nemophila*.

Thus were separated closely related forms which agree overwhelmingly in their distinctive succulent and scandent or reclining habit, their prickly stems and spiny capsules, the regular markings of their ecucullate globose seeds, and their geographical distribution. Even though a considerable upheaval in nomenclature necessarily results, this separation does violence to avowed aims of phylogenetic taxonomy, or systematic botany, and must be corrected. Greene (1894) was apparently the first writer to perceive the close affinity between these species. Accordingly, he combined them under *Nemophila*. In this position, however, they form a unit whose aberrant features jeopardize the homogeneity of that genus. *Ellisia* would be similarly affected were they all to be placed in that group.

The definite pattern of the seed coat, the absence of a cucullus and the enlargement of the persistent calyx in fruit relate *Pholistoma* to *Ellisia*, proper. *Ellisia Nyctelea*, however, has a delicate, non-succulent, non-scandent habit, lacks the prickles on the stem and capsule, has a short and narrow corolla usually shorter than the calyx, and differs fundamentally in geographical range. All of these conditions indicate that the existing

[1] Part of the expense of publication borne by the author.

[THE BULLETIN FOR MAY (66: 263–339) WAS ISSUED MAY 4, 1939]

discrepancy between the two genera demands consideration. The several-flowered, secund, cymose inflorescence of *Pholistoma* finds a counterpart in that of *Eucrypta* Nutt., but the distinctive features of that genus, already pointed out (Constance, 1938), preclude the incorporation of these two groups. The only species to share the prickly armature of the stem with *Pholistoma* is *Nemophila breviflora* Gray, which has cucullate, pitted seeds and other divergent characters which argue strongly against any close relationship.

It has been proposed (Constance, 1939) to take up *Pholistoma* Lilja, and to erect it as a genus embracing the segregated elements in question. Although this name is infrequent in botanical literature, it was validly published and adequately identified by a type species and so is the mandatory designation for the group if it is not to be retained in either *Ellisia* or *Nemophila*. Lilja, in founding this genus, laid stress upon the angled corolla-tube and broad corolla-scales of *Pholistoma auritum*, the type species. These characters have, apparently, only specific value. The name is derived from the Greek words, *pholis*, a scale, and *stoma*, a mouth, in reference to the fact that the squamae sometimes conspicuously occlude the mouth of the corolla-tube. This treatment, it is believed, will adequately circumscribe and define a natural alliance of species and, at the same time, relieve both *Ellisia* and *Nemophila* of species whose inclusion would merely serve to destroy their genetic unity.

The present geographical distribution of the species may afford a clue to the origin of the genus. The range of *Pholistoma racemosum* and *P. membranaceum*, and the combined ranges of *P. auritum* and var. *arizonicum*, are largely comparable to those of several living species represented by fossil equivalents in the Miocene Tehachapi Flora. Axelrod (1939) attributes a northern Mexican origin to these modern species. It is not improbable that *Pholistoma* may have developed in this area and later spread to the north and east to occupy its present range.

The writer is indebted to Dr. W. L. Jepson for the opportunity of examining critical specimens in his working herbarium of the Californian flora, and to Dr. Mildred E. Mathias and others for the gift of a number of significant collections. Professor Milo S. Baker, Kenwood; Mr. Ira W. Clokey, South Pasadena; Dr. Robert F. Hoover, Berkeley; and Mr. Frank W. Peirson, Altadena, have generously made avilable the specimens of this genus in their private herbaria. The curators of the following important collections have kindly loaned for study the specimens in their care: California Academy of Sciences, San Francisco (CA); Cornell University, Ithaca (CU); Field Museum of Natural History, Chicago (F); Gray Her-

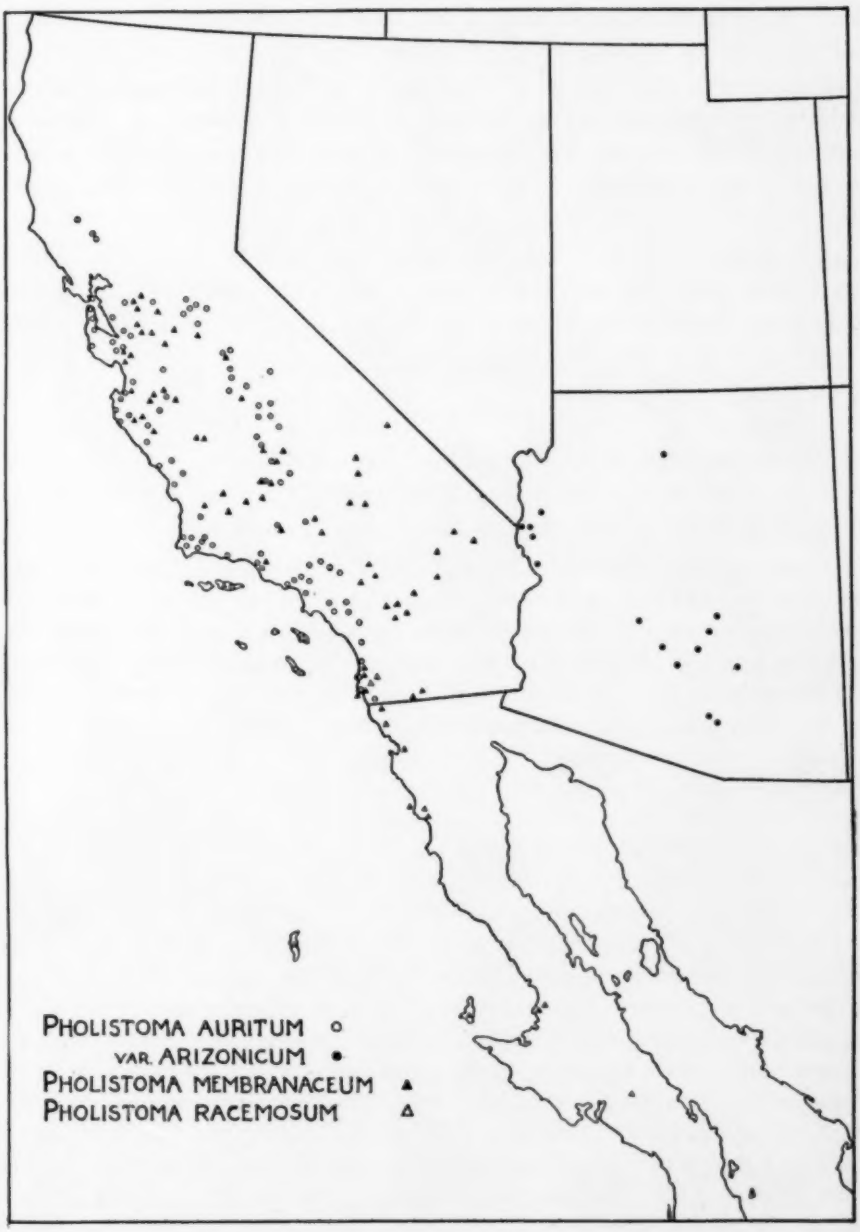


Fig. 1. Geographical Distribution of *Pholistoma*.

barium of Harvard University, Cambridge (G); Royal Botanic Gardens, Kew (K); Missouri Botanical Garden, St. Louis (M); New York Botanical Garden, New York (NY); Oregon State College, Corvallis (OS); Pomona College, Claremont (P); Academy of Natural Sciences, Philadelphia (PA); Rocky Mountain Herbarium of the University of Wyoming, Laramie (RM); Dudley Herbarium of Stanford University (S); University of California, Berkeley (UC); University of Oregon, Eugene (UO); United States National Herbarium, Washington (US); University of Washington, Seattle (UW); Vegetation Type Map Herbarium of the California Range and Forestry Experiment Station, Berkeley (VTM); State College of Washington, Pullman (WS).

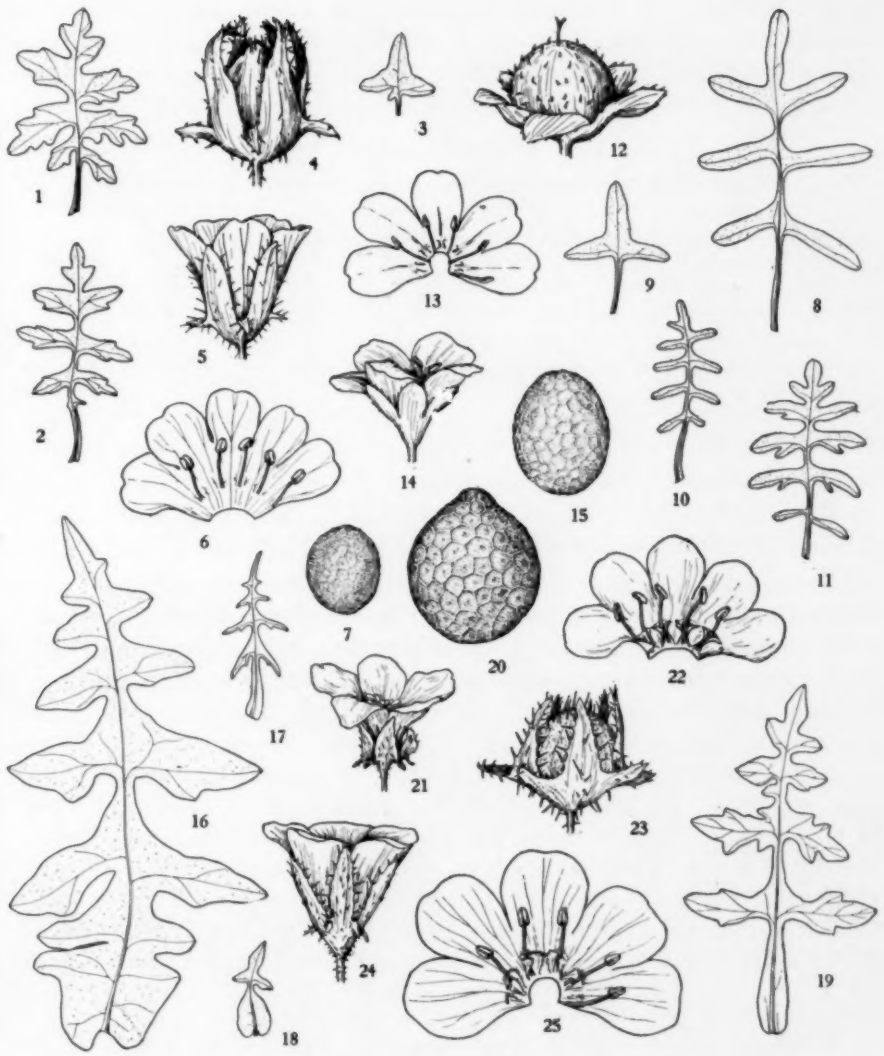
TAXONOMIC TREATMENT

PHOLISTOMA Lilja

Pholistoma Lilja; in Lindblom, Bot. Notiser, 40. 1839.

Nemophila Nutt., *Ellisia* L., *Macrocalyx* Trew, and *Nyctelea* Scop., all of subsequent writers, in part, not of the original authors!

Green or glaucous succulent annual herbs, at first simple, but soon much branched and reclining upon other plants or upon the ground. Stems succulent and brittle, angled and the angles armed with unciniate prickles, hispidulous or glabrate. Cotyledons with an oval or orbicular blade, truncate at base, on slender petioles of greater length, usually deciduous before full anthesis. Lowest leaves opposite, the others alternate, oblong, ovate-lanceolate or ovate-deltoid, cordate or truncate at base and pinnately divided into lanceolate. oblong or ovate acute or obtuse lobes which are entire or few-toothed, slightly succulent or thin and membranous, venose, more or less hispidulous on both surfaces and bristly or prickly on the margins and on the veins below; uppermost leaves reduced and short-petioled, often deltoid, 3-lobed; stomata confined to the paler lower surface or a few on the veins above; petioles narrowly or broadly winged, slightly dilated and connate-clasping at the base or broadly flaring and auriculate, equalling or shorter than the blades. Flowers solitary in the axils or several in few-bracteate, semi-secund, raceme-like cymes which arise in the axils or opposite the alternate leaves or terminally. Calyces broadly campanulate, 5-cleft nearly to the base into linear-lanceolate to oval acute or obtuse lobes, these more or less hispidulous on both surfaces and bristly-ciliate; sinuses provided with auricles resembling the sepals in form, or sinuses naked. Corollas bowl-shaped or semi-rotate, white, blue or violet, the oval to obovate lobes exceeding the tube, the whole exserted from the calyx; corolla-scales a pair at the base of each filament, broad and triangular or narrow or minute, a nectary between each pair. Stamens included but slightly exceeding the corolla-tube, anthers oblong- or ovate-cordate. Pollen grains smooth, tricolpate. Styles cleft less than one-half. Mature capsules globose, armed with stout bristles



CONSTANCE: PHOLISTOMA

Explanation of Plate 7.

Figs. 1–7. *P. racemosum:* Figs. 1–3, leaves ×½; Fig. 4, fruiting calyx ×3; Figs. 5, 6, corolla ×3; Fig. 7, seed ×7½.

Figs. 8–15. *P. membranaceum:* Figs. 8–11, leaves ×½; Fig. 12, fruiting calyx ×4; Figs. 13, 14, corolla ×3; Fig. 15, seed ×7½.

Figs. 16–23. *P. auritum:* Figs. 16–19, leaves ×½; Fig. 20, seed ×7½; Figs. 21, 22, corolla ×1; Fig. 23, fruiting calyx ×2.

Figs. 24, 25. *P. auritum arizonicum*, corolla ×3.

or prickles, exceeded by the enveloping or stellate-spreading, strongly accrescent calyx, loculicidally dehiscent by two valves. Seeds mostly 1–6, homomorphic, globose, light brown, regularly alveolate or reticulate. Cucullus none. Type species: *Pholistoma auritum* Lilja (*Nemophila aurita* Lindl.).

KEY TO THE SPECIES

Foliage green; calyx with conspicuous auricles, enveloping the mature capsule; capsule 5–10 mm. in diameter.
  Cauline leaves auriculate-clasping; corolla-scales broad and conspicuous.
    Corolla usually 1–3 cm. broad; California ..... *P. auritum.*
    Corolla usually less than 1 cm. broad; Arizona ..... var. *arizonicum.*
  Cauline leaves with narrowly winged but only slightly connate petioles; corolla-scales usually narrow and inconspicuous; corolla mostly less than 1 cm. broad ..... *P. racemosum.*
Foliage glaucous; calyx without auricles, stellate-rotate under the mature capsule; capsule 2–4 mm. in diameter ..... *P. membranaceum.*

PHOLISTOMA AURITUM (Lindl.) Lilja

Nemophila aurita Lindley, Bot. Reg. **19:** t. 1601. 1833.
Pholistoma auritum Lilja; in Lindblom Bot. Notiser, 40. 1839.
Viticella aurita Macbride, Contr. Gray Herb. **59:** 29. 1919.

Foliage green; stems 2–12 dm. long. sparingly hispidulous; blades of the cotyledons 8–10 mm. in diameter; lower leaves oblong to ovate-lanceolate, 8–15 cm. long, 2–8 cm. broad, acuminate at apex, cordate at base, divisions 7–13, oblong or lanceolate, falcate or retrorse, obtuse or acute, entire or 1–5-toothed, more or less hispidulous on both surfaces; petioles broadly winged and auriculate-clasping; flowers solitary or 2-6 in cymes; calyx-lobes lanceolate or ovate-lanceolate, 4–8 mm. long, 2–2.5 mm. broad, auricles similar, 1–2 mm. long, corolla 1–3 cm. broad, lavendar to blue or violet with darker markings at the throat, the oval or obovate lobes somewhat erose and often pubescent distally, the short tube paler, angled and slightly coarctate at the throat; corolla-scales purple, 3-angular, the free edge often fimbriate, the yellow nectaries conspicuous; anthers 1.5 mm. long; style about 5 mm. long; capsule 5–10 mm. in diameter, enclosed by the calyx; seeds 1–4, 2–3 mm. in diameter.

Type locality: "found in California," *Douglas.*

Range: Coast Ranges of California from San Diego County to San Francisco Bay and Lake County; San Clemente and Santa Catalina islands; Sierra Nevada foothills from Kern County to Calaveras County; Upper Sonoran and Arid Transition life zones.

Representative material: CALIFORNIA. Locality uncertain: "California," *Douglas* (K: type of *Nemophila aurita*, G,NY), *Bridges 170* (G,NY,UC, US); without locality, *Coulter 471* (G,K). Lake Co.: Clear Lake, 1933, *M. S. Baker 7518* (Baker,CA); Sulphur Banks, 1901–2, *Bowman 270* (G,S). Marin Co.: Angel Island, *Rattan* (S), 1888, *Chesnut* (UC). Contra Costa Co.: Alamo Canyon, 1932, *Bowerman 1089* (UC); Lake Chabot,

1904, *Osterhout & Gardner* (UC). Alameda Co.: Niles Cañon, 1891, *Chesnut & Drew* (P,UC,UO); Oakland, 1860–7, *Bolander 152* (F,M); San Leandro, 1877, *H. Edwards* (CA,NY); Sunol, 1938, *Constance 2231.* San Francisco Co.: South San Francisco, 1892 *E. Cannon* (CA). San Mateo Co.: Burlingame, 1925, *J. Campbell* (CU); Pescadero Creek, 1928, *C. Meyer 376* (UC). Santa Clara Co.: Stanford University, 1902, *Abrams 2309* (G,M, NY,P,RM,S), 1902, *C. F. Baker 399* (CA,F,G,M,NY,P,RM,S,UC,US, WS); Stevens Creek, 1907, *Heller 8516* (F,G,M,NY,PA,S,US). Monterey Co.: Abbotts, 1938, *Constance & Hoover 2060;* Del Monte, 1903, *Heller 6683* (CA,F,G,M,NY,P,PA,RM,S,UC,US); Santa Lucia Mountains, 1898, *Plaskett 81* (G,NY,US). San Benito Co.: Pinnacles, 1929, *Mexia 2364* (CA, UC,US); Tres Piños River, 1921, *Abrams & Borthwick 7845* (S). San Joaquin Co.: Stockton, *Stanford 188* (UC). Stanislaus Co.: Knights Ferry, 1938, *Constance 2195;* Modesto, 1935, *Hoover 369* (Hoover, UC). Merced Co.: Pacheco Pass, 1925, *Abrams 10747* (S), 1938, *L. Koch 159* (Baker, UC) Calaveras Co.: Robinson's Ferry, 1854, *Bigelow* (G,NY,PA,US); Table Top Mountain, 1936, *Belshaw 1897* (VTM). Tuolumne Co.: Columbia, 1916, *A. L. Grant 679* (Jepson); Iron Cañon, 1919, *Ferris 1661* (CA,NY, S,US). Mariposa Co.: Mariposa Creek, 1938. *Constance & Mason 2128;* Pea Ridge Road, 1903, *Congdon* (US). Madera Co.: Kelshaw Corners, 1938, *Constance 2201;* Pollasky, 1906, *Heller 8147* (CA,F,G,M,NY,PA,S, US). Fresno Co.: Squaw Valley, 1938, *Constance 2224;* Tollhouse, 1938, *Constance 2214.* Tulare Co.: Exeter, 1930, *Parks & Parks 0423* (CA,M, NY,P,UC), 1938, *Constance & Mason 2105;* Oak Grove, 1925, *Bacigalupi 1217* (NY,P,S). Kern Co.: Caliente, 1938, *Mathias 1344* (UC); Hobo Hot Springs, 1938, *Constance & Mason 2119;* Kern Canyon 1938, *Mathias 1346* (UC). San Luis Obispo Co.: Cambria, 1926, *Eastwood 13609* (CA); San Luis Obispo, 1882, *Summers* (UC,US). Santa Barbara Co.: Dos Pueblos, 1861, *Brewer 396* (UC,US); Los Alamos Creek, 1920, *Jepson 8449* (Jepson); Santa Barbara, 1902, *Elmer 3942* (M,NY,P,S,US); "St. Barbara," *Nuttall* (K,PA); Santa Cruz Island, 1888, *T. S. Brandegee* (UC), 1930, *Abrams & Wiggins 109* (CA,F,G,S,UC). Ventura Co.: Casitas Pass, 1902, *H. M. Hall 3136* (NY,S,UC,UO,US); East Casitas Pass, 1931, *C. Wolf 2032* (S,UC). Los Angeles Co.: Claremont, 1917, *Johnston 1249* (Clokey,P,S); Los Alisos Canyon, 1931, *Epling* (CA,M,OS,S,UC,US); Los Angeles, 1888–9, *Hasse* (M,NY,S); Los Flores Canyon, 1930, *Epling & Ellison* (M,OS,PA,UC,US); Mandeville Canyon, 1929, *Clokey & Templeton 4437* (Clokey,CU,G,M,NY,P,UC), 1930, *Epling* (F,M,OS,UC,US); "Pueblo de los Angeles," *Gambel* (G); San Clemente Island, 1903, *Trask 201* (NY,US), 1923, *Munz 6663* (P,UC); Santa Catalina Island, 1901, *Trask 456* (F,NY), 1904, *G. B. Grant 832* (G,M,RM). Orange Co.: Santa

Ana Cañon, 1926, *M. E. Jones* (G,S); Silverado Cañon, 1920, *Munz & Harwood 3725* (P,US). Riverside Co.: Murietta, 1916, *Robinson & Crocker* (M,P); Prado, 1920, *Barrus & Whetzel 249* (CU). San Diego Co.: Fallbrook, 1882, *M. E. Jones 3095* (CA,Clokey,M,NY,P,S,US); La Jolla, 1914, *Clements & Clements 96* (F,G,M,NY,PA); San Diego, 1850, *Parry* (NY,US), 1916, *Spencer 107* (G,NY,UC,US); San Pasqual, 1852, *Thurber 604* (F,G,NY); Ysidora, 1903, *Abrams 3290* (F,G,M,NY,P,PA,S,US).

The plants vary greatly in size, foliage, corollas and fruits, but except var. *arizonicum* no variant populations have, as yet, been described. The stems often attain a great length, climbing up through and over shrubs by means of their efficient recurved prickles. The almost rotate limb, angled tube and conspicuous nectaries give this species a striking appearance. The color of the corolla fluctuates over a wide range of hues and intensities, from very pale to deep blue, and from light to dark violet.

To date, no specimens of *P. auritum* have been reported from Mexico, although it occurs so close to the international boundary as to make its subsequent discovery in Baja California highly probable.

Pholistoma auritum var. **arizonicum** (M. E. Jones) n. comb.

Nemophila arizonica M. E. Jones, Contr. West. Bot., **12:** 50. 1908.

N. aurita var *arizonica* Brand, Pflanzenr. IV. 251. 45. 1913.

Closely similar to the species, but usually smaller, more slender and less prickly throughout; divisions of the leaves fewer and very blunt; corollas usually less than 1 cm. broad, about equalling the calyx.

Type locality: "Chimihuevis Mountains, Arizona" (Mohave County), 1903, *M. E. Jones.*

Range: mountains of western and south-central Arizona.

Representative material: ARIZONA. Mohave Co.: Chimihuevis Mountains, 1903, *M. E. Jones* (P: type of *Nemophila arizonica*); Fort Mohave, 1884, *Lemmon* (UC); Yucca, 1884, *M. E. Jones* (P,PA). Coconino Co.: Diamond Creek Cañon, 1893, *Wilson* (UC); Hermit Creek, 1917, *Eastwood 6024* (CA). Gila Co.: Roosevelt Dam, 1917, *Eastwood 6259* (CA); Winkelman, 1922, *Wiegand & Upton 4080* (CU). Maricopa Co.: Salt River Mountains, 1932, *Gillespie 8849* (G,S,UC,US); Stewart Mountain, 1935, *Peebles 10656* (F,US); Tortilla Flat, 1935, *Nelson & Nelson 1761* (M,NY,RM); White Tank Mountains, 1932, *Gillespie 8876* (NY,P,S,US). Pinal Co.: Desert Wells—Stewart Mountain, 1932, *Gillespie 5451* (NY,P, S,UC,US); Superstition Mountain, 1937, *Peebles, Harrison & Kearney 3704* (US). Pima Co.: Alamo Well, 1933, *Wiggins 6527* (S,US); Sierra Tucson, 1884, *Pringle* (F,G,M,NY,PA,UC,US).

The consistently smaller and often paler corollas, the blunt leaf-lobes, and the Arizonan distribution mark this as a valid geographical variant of *P. auritum* and warrant its retention in varietal status. The size of the flowers suggests those of *P. racemosum*, with which it has sometimes been confused, but the flaring petioles and broad scales relate it to *P. auritum*. Despite the sharp discontinuity in distribution between the species and its variety, morphological agreement is too close to allow of specific separation.

Pholistoma racemosum (Nutt.) n. comb.

Nemophila racemosa Nuttall ex Gray, Proc. Amer. Acad. **10:** 315. 1875.

Viticella racemosa Macbride, Contr. Gray Herb. **59:** 30. 1919.

Nemophila erodiifolia Millspaugh ex Millspaugh & Nuttall, Field Mus. Publ. 312. Bot. Ser. **5:** 205. 1923.

Foliage green; stems 3–6 dm. long, sparingly hispidulous or glabrate; blades of the cotyledons 6–9 mm. in diameter; lower leaves ovate or deltoid-ovate in outline, 4–10 cm. long, 2–6 cm. broad, obtuse at apex, subcordate or truncate at base, divisions 5–9, oblong or ovate, obtuse or acute, entire or 3–5-toothed, more or less hispidulous on both surfaces, more densely so beneath; petioles narrowly winged and not auriculate; flowers solitary or usually 2–6 in cymes; calyx-lobes linear- or ovate-lanceolate, 2–3 mm. long, 1–1.5 mm. broad, auricles similar, 1–1.5 mm. long; corolla 0.6–1 cm. broad, white or blue, the obovate lobes often pubescent distally; corolla-scales 3-angular but usually narrow or obsolete, the upper portion often free and fimbriate; anthers 0.6 mm. long; style about 2.5 mm. long; capsule 5–8 mm. in diameter, enclosed by the calyx; seeds usually 4–6, sometimes solitary, 1–2 mm. in diameter.

Type locality: "California; San Diego, *Nuttall*."

Range: San Diego and Baja California coast; Santa Cruz, San Clemente, Santa Catalina, San Martin, Cedros and Guadalupe islands.

Representative material: CALIFORNIA. Santa Barbara Co.: Santa Cruz Island, 1888, *T. S. Brandegee* (F,UC), 1930, *Abrams & Wiggins 1* (CA,F, G,S,UC), 1930, *Clokey 5033* (Clokey,G,NY). Los Angeles Co.: San Clemente Island, 1885, *Nevin & Lyon* (G,S), 1903, *Trask 200* (NY,US), 1923, *Munz 6646* (G,P,UC). Santa Catalina Island, 1893, *McClatchie 349* (F, NY), 1900–4, *G. B. Grant 831* (F,G,M,PA,RM,S,UC), 1920, *Millspaugh 4687* (F: type of *Nemophila erodiifolia*), 1921, *E. C. Knopf 13* (F,US). San Diego Co.: La Jolla, 1914, *Clements & Clements 97* (F,G,M,NY,PA), 1929, *Parks & Parks 0339* (CA,G,M,NY,P,RM,S,UC); Mission Hills, 1903, *Abrams 3431* (G,M,NY,P,S); Point Loma, 1913, *Eastwood 2563* (CA, Clokey, G,NY,US); San Diego, 1882, *M. E. Jones 3056* (CA,Clokey,G, M,NY,P,US); "St. Diego," *Nuttall* (G: type of *Nemophila racemosa*, K): Tia Juana, 1913, *Eastwood 2922* (CA,G,US).

BAJA CALIFORNIA. San Quintin, 1935, *Epling & Robison* (NY,S,UC); Santo Domingo, 1930, *Wiggins 4294* (NY,S,UC), *4506* (S,UC); Todos Santos Bay, 1885, *Orcutt 1259* (G,M,US); Cedros Island, 1897, *T. S. Brandegee* (NY,UC); San Martin Island, 1897, *Anthony 229* (G,M,S,US); Guadalupe Island, 1875, *Palmer 76* (M,NY,PA), 1889, *889* (G,US), 1885, *Greene* (G,S,UC), *Anthony 254* (F,G,M,P,S,UC,US), 1892–3, *Franceschi 32* (F,M,UC,US), 1911, *J. N. Rose 16017* (NY,US).

Nemophila erodiifolia was separated because it had blue or bluish, instead of white corollas and more than one seed in each capsule instead of solitary seeds. Perhaps the emphasis upon seed-number was due to Brand's belief that *P. racemosum* always has only one seed in each capsule, although some of the specimens he cites show as many as eight or nine seeds. Color of the corolla is notoriously variable in the entire tribe and so cannot lend weight to this segregate, which is without taxonomic significance.

Pholistoma membranaceum (Benth.) n. comb.

Ellisia membranacea Bentham, Trans. Linn. Soc. Lond. **17:** 274. 1834.
Macrocalyx membranaceus O. Kuntze, Rev. Gen. **1:** 434. 1891.
Nemophila membranacea Greene, Man. Bay-Reg., 252. 1894.
Ellisia membranacea var. *hastifolia* Brand, Pflanzenr. IV. 251. 38. 1913.
Nyctelea membranacea Tidestrom, Proc. Biol. Soc. Wash. **48:** 42. 1935.

Foliage glaucous; stems 0.5–6 dm. long, glabrous; blades of the cotyledons usually 4–7 mm. in diameter; lower leaves oblong to oval, 3–12 cm. long, 1–5 cm. broad, obtuse at apex, subcordate or truncate at base, divisions 5–11, oblong, obtuse, rather distant and entire or with a single broad lateral tooth, sparsely hispidulous on both surfaces; petioles more or less winged but not auriculate; flowers 2–10 in cymes, or rarely solitary: calyx-lobes oval, 2–3 mm. long, 1–2 mm. broad, obtuse, auricles 0; corolla 0.4–1 cm. broad, white and often with a lanceolate purple spot on each lobe, the lobes oval; corolla-scales 3-angular, very small and entire; anthers 0.4–0.6 mm. long; style 1.5–2 mm. long; capsule 2–4 mm. in diameter, the fruiting calyx stellate-spreading beneath it; seeds 1–2, 2–3 mm. in diameter.

Type locality: "from Mr. Douglas' Californian collection."

Range: Coast Ranges from Baja California to Contra Costa County; Sierra Nevada foothills from Mariposa County south and east through the desert ranges to Inyo and San Bernardino counties; absent from the islands and usually from the immediate coast; Upper and Lower Sonoran life zones.

Representative material: CALIFORNIA. Locality uncertain: "California," 1833, *Douglas* (K: type of *Ellisia membranacea*, G), *Coulter 470* (G,K,NY); "Southern California," 1876, *Parry & Lemmon 257* (F,NY). Contra Costa Co.: Antioch, 1868–9, *Kellogg & Harford 788* (CA,G,NY-

part); Nortonville, 1929, *Mason 5046* (UC). Alameda Co.: Cedar Mountain, 1903, *Elmer 4438* (CA,M,NY,OS,P,S,UC,UO,US: isotypes of *Ellisia membranacea* var. *hastifolia*); Corral Hollow Road, 1930, *Stanford 1397* (CA,G,M); Patterson Pass, 1933, *L. S. Rose 33057* (CA,F,M,P,S,UC). Santa Clara Co.: Edenvale, 1917, *Abrams 6400* (Clokey,NY,P,S,UW); Evergreen, 1893, *Davy 52* (RM,S,UC); Pacheco Pass, 1938, *L. Koch 158* (Baker,UC). Monterey Co.: Big Pinnacles, 1925, *Ferris 4120* (P,S); Jamesburg, 1929, *Mason 5039* (UC), 1938, *Constance & Hoover 2054;* Jolon, 1935, *Wiggins, 8029* (S,UC). San Joaquin Co.: Castle Rock, 1938, *Hoover 2792* (Hoover,UC). Stanislaus Co.: Arroyo del Puerto, 1935, *Sharsmith & Sharsmith 1553* (UC), *Ferris 9051* (CA,NY,S,UC); LaGrange, 1937, *Hoover 1706* (Hoover,UC). San Benito Co.: Emmet—Panoche Pass, 1921, *Abrams & Borthwick 7908* (NY,P,S); Gabilan Range, 1938, *Constance & Hoover 2065;* Glaucophane Ridge, 1938, *Constance & Hoover 2072;* The Pinnacles, 1930, *J. T. Howell 4616* (CA,G,US). Mariposa Co.; Lewis, 1892, *Congdon* (S). Fresno Co.: Alcalde, 1891, *T. S. Brandegee* (UC,US); Alcalde Canyon, 1938, *Hoover 2944* (Hoover,UC); Jacalitos Canyon, 1931, *J. T. Howell 5823* (CA). Tulare Co.: Exeter, 1930, *Parks & Parks 0436* (UC,US), 1938, *Constance & Mason 2102;* Middle Tule River, 1892, *Purpus 5080* (G,UC,US). Kern Co.: Caliente, 1905, *Heller 7612* (F,G,M, NY,P,PA,S,UC,US); Fort Tejon, 1857–8, *Xantus 88* (G,NY,PA,US); Kern River Canyon, 1938, *Mathias 1320* (UC), *1321* (UC), *1322* (UC); Tehachapi Pass, 1925, *Munz 8978* (P,UC). Inyo Co.: Funeral Mountains, 1891, *Coville & Funston 332* (CU,G,M,NY,PA,S,US); Great Falls Canyon, 1930, *Epling, Ellison & Anderson* (F,OS,US). San Bernardino Co.: Bonanza, 1920, *Munz & Harwood 3430* (P,US); Kelso, 1906, *M. E. Jones* (G,P,S); Lava Mountains, 1938. *Constance & Mason 2113;* Morongo Valley, 1928, *J. T. Howell 3404* (CA,G,NY,S,US). San Luis Obispo Co.: Bitterwater Valley, 1932, *Wiggins 5798* (NY,P,S,UC); Cuyama, 1896, *Eastwood* (G,UC); Paso Robles, 1938, *Constance 2085*. Ventura Co.: Road to Ojai, 1935, *Munz 13597* (P,S,UC). Los Angeles Co.: Antelope Valley, 1895, *Davidson* (S). Riverside Co.: Cabezon, 1881–3, *Parish & Parish 21* (F,Jepson,M,NY,PA,S,UC,UO,US,WS); Palm Canyon, 1930, *Spencer 1582* (G,P); Tahquitz, 1919, *Peirson 981* (Peirson); Whitewater, 1881, *Vasey* (PA,UC). San Diego Co.: Bernardo, 1903, *Abrams 3375* (F,G,M, NY,P,PA,S,UC,US); Coyote Cañon, 1902, *H. M. Hall 2813* (M,NY,S,UC, US); La Jolla, 1904, *Chandler 5129* (NY,S,UC); Ocean Beach, 1917, *Spencer 276* (G,NY,P); San Diego, 1849–50, *Parry* (NY,PA,US), 1875, *Palmer 244* (F,M), 1882, *M. E. Jones 3082* (Ca,Clokey,G,M,NY,P,S,US), *Pringle* (F,G,UO,US); "St. Diego," *Nuttall* (PA).

BAJA CALIFORNIA. San Quintin, 1889, *Palmer 638* (CA,F,G,NY,PA, US); Santo Domingo, 1930, *Wiggins 4288* (NY,S,UC); Tia Juana, 1882, *Orcutt 295* (US).

Variety *hastifolia* is a sporadic and trivial foliar variant without either correlated characters or geographical significance and is hence of no taxonomic worth. *P. membranaceum* agrees closely with the preceding species in habit, foliage and seeds, but its usually more complex inflorescence and its rotate fruiting calyx, without any trace of auricles, render it somewhat anomalous and give it a superficial resemblance to *Eucrypta*. Equally at home in the live-oak belt of the inner south Coast Ranges and with *Larrea* in desert areas, this species has occupied a range which is more definitely interior than that of either *P. auritum* or *P. racemosum*.

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Secondary Vascular Tissues of the Oaks Indigenous to the United States—I. The Importance of Secondary Xylem in Delimiting Erythrobalanus and Leucobalanus

SIMON WILLIAMS

(WITH SIX FIGURES)

INTRODUCTION

The original objective sought in this research was to determine whether it was practicable to attempt the identification of the species of *Quercus* native to the United States, on the basis of anatomical variations occurring in the secondary xylem; some progress has been made in this direction, and these results will be published at a later date. As the study of oak woods has progressed, however, it has become increasingly evident that considerable confusion exists in the taxonomy of the genus, a situation which has been further emphasized through the compilation of certain anatomical data, the seeming logical interpretation of which is in direct variance with existing classification. The present paper has been written in the hope that it may be of some service in clarifying the taxonomy of the genus.

If the identification of the various species of oak on the basis of wood structure is to be followed to its logical conclusion, it is patent that a trustworthy classification of the species within the genus must be available which can serve as a logical starting point. Furthermore, to reap the greatest benefits from the study, this classification must be one accepted by all leading taxonomists. A survey of the literature (4, 5, 6, 12, 17, 18, 19, 20, 24) has revealed that no such situation exists, that the taxonomy now employed in *Quercus* has inordinately magnified the natural complexities of this large group. The following paragraphs will serve to show the situation as it now exists in so far as it is concerned with the limits of subgenera.

CONCEPTS OF SUBGENERA IN QUERCUS

The concept of subgenera in *Quercus* is of genuine value, and certain natural groups of species within the genus have long been recognized by systematists (8, 19). As interpreted at present, two of these, ERYTHROBALANUS Spach, and LEUCOBALANUS Engel. (the red and white oaks, respectively), include all of the species native to the United States. CYCLOBALANUS Endl., CYCLOBALANOPSIS Benth. & Hook., and CHLAMYDOBALANUS Endl., are restricted to the Orient and hence do not fall within the scope of this paper.

With the concept of ERYTHROBALANUS and LEUCOBALANUS there is no dispute. The confusion exists, rather, in the efforts made to define the

boundaries of these subgenera, and in assigning species to them. The red and white oaks originally were grouped in LEPIDOBALANUS by Endlicher. Later Spach and then Liebmann, among others, split off ERYTHROBALANUS. In 1877, Engelmann (8) place the oaks in two sub-sections, LEUCOBALANUS (white oaks) and MELANOBALANUS[1] (black oaks); his paper is of particular interest since it serves to emphasize the difficulties that have always confronted systematists in selecting a set of characters that would successfully delimit the two natural groups and avoid flagrant exceptions. For example, Engelmann found it quite difficult to orient satisfactorily certain species in a manner at once logical and at the same time retain their natural affinities. Thus, LEUCOBALANUS, defined as having basal or rarely lateral abortive ovules, 6 to 8 stamens, sessile or subsessile stigmatic surfaces, and the inner surface of the acorn shell glabrous or rarely tomentose, includes in Engelmann's first arrangement such a species as *Q. emoryi* Torr. In a subsequent grouping later in the same paper, this species is listed with the black oaks, defined as having apical abortive ovules, 4 to 6 stamens, elongated recurved styles, and the inner surface of the acorn shell tomentose. Nevertheless, Engelmann's astuteness should not be overlooked for, despite the paucity of his species complement, he did so define the two subgroups that no exceptions occurred as regards any major definitive feature. Mention should be made at this time that Engelmann, either by design or by accident, failed to use acorn maturation as a major feature in separating the two groups, relegating this feature to secondary rank, common to both. It is difficult to understand why taxonomists since 1877 have deliberately altered Engelmann's concept of subgeneric limits, in this way creating an anomalous situation which cannot but cast considerable suspicion upon the validity of the present groupings.

A careful examination of the features now generally used in defining the limits of LEUCO- and ERYTHROBALANUS reveals the fact that no one character is used which is not duplicated in one or more species in the alternate subgenus. Taxonomists, by readjusting the emphasis to be placed on the various features listed by Engelmann, and by shifting various species between the two subgenera, have created exceptions that defeat the logic of the rule. The situation can best be stressed by resorting to an illustration, the interpretation of which calls for a summation of the features which, at present, characterize the red and white oaks, respectively.

CRITICAL ANALYSIS OF TABLE 1

Attention may now be focussed to advantage on the position accorded *Q. emoryi* Torr. and *Q. agrifolia* Nee, by taxonomists. With the exception

[1] ERYTHROBALANUS is commonly used in defining this group at the present time.

of Trelease's work (9), modern references list *Q. emoryi* as a white oak; *Q. agrifolia* is a red oak by unanimous consent. The logic of this procedure is open to question. *Q. emoryi* matures its acorn in one year, but the same holds for *Q. agrifolia*. Both may exhibit leaves with spinose teeth. The stigmatic surfaces are similar, that is, they are of the red oak type (4 under ERYTHROBALANUS in Table 1). The inner wall of the acorn shell is tomentose in each. Actually, the only distinction which holds between the two species is the position of the abortive ovules; these are basal in *Q. emoryi* and apical in *Q. agrifolia*. Can this feature, then, be considered as infallable for the ultimate segregation of *Quercus* species into the sub-

TABLE 1

Features characterizing Erythrobalanus and Leucobalanus as interpreted at present

ERYTHROBALANUS	LEUCOBALANUS
1—Acorns mature in two years.	1—Acorns mature in one year.
2—Inner surface of acorn shell tomentose.	2—Inner surface of acorn shell glabrous.
3—Leaves or their lobes bristle-tipped, or with spiny teeth.	3—Leaves or their lobes neither bristle-tipped, nor with spiny teeth.
4—Styles elongated, finally recurved; stigmatic surfaces gradually dilated.	4—Styles short; stigmatic surfaces abruptly expanded.
5—Abortive ovules apical.	5—Abortive ovules basal.

genera? Apparently not, for *Q. chrysolepis* Liebm. and *Q. tomentella* Engel., which are conceded by taxonomists to be red oaks, show basal abortive ovules. For what reason is *Q. emoryi* classified as a white oak; why *Q. agrifolia* as a red oak? On what basic standards have *Q. chrysolepis* and *Q. tomentella* been classified? The answer is obviously debatable, as is indicated by conflicting expressions of opinion in modern references. Trelease, for example, lists *Q. emoryi* as a red oak in contrast to all other authors, and places *Q. chrysolepis* and *Q. tomentella* in a third subgenus, PROTOBALANUS, a division which has not found favor with other systematists (24). Sargent, in his Silva (19) and Manual (20) reverses the position of the latter two species, apparently basing his decision upon similar data.

It is admitted that these exceptions to the rules upon which the subgenera are based are few in number. Nevertheless, they are exceptions, and for this very reason seriously hamper the effectiveness of this classification. Illustrating as they do the lack of infallible criteria for assigning species to one or the other subgenus, their anomalous position points to an important flaw in the present classification, particularly if this is to indicate natural affinities.

THE RÔLE OF WOOD ANATOMY IN CLASSIFICATION

As stated previously, it has become increasingly evident that some of the data accumulated in the comparative anatomical study of the *Quercus* species could be used to advantage in clarifying the confusion now existing within the genus, particularly as regards the precise limits of ERYTHRO- and LEUCOBALANUS. The interpretation of anatomical data as an aid in solving difficult taxonomic problems is relatively new, but this tool has already proven of undisputed value, which justifies its introduction into the present discussion (9, 11, 15, 23, 25, 27).

Systematists will be forced to go beyond the traditional use of floral organs and their derivative parts (fruits, seeds, etc.), if natural relationships and phylogenetic trends are to be clearly established among plants. In assaying the importance of the above-mentioned features to their full value, overemphasis has resulted, and many unjustified taxonomic problems have arisen as a result. The persistent use of acorn maturation in defining the red and white oak groups illustrates this point. If further progress is to be made, data compiled by the taxonomist, the anatomist, the cytologist, the geologist, the geneticist, etc., must all be correlated and the information weighted according to the particular problem.

Leading taxonomists are already committed to the idea that anatomy serves as an accurate guide in defining the limits of the larger natural units of vegetation, that is, the family, the genus, and in this instance, the subgenus. Differences between species are less prone to be as significant as the above, and usually are the result of insufficient sampling. There is no indication that external differences between closely related species necessarily imply internal differences. This does not mean that differences never occur between species, but if these are present, exceptional care must be exercised to test adequately their validity. It is imperative that in the continued acceptance of wood anatomy as a taxonomic tool, negative evidence be as clearly exposed and weighed as positive evidence. If high standards are to be demanded of the systematist, equally high standards must be met by the applied botanist.

EVIDENCE OF SUBGENERIC LIMITS PRESENTED BY ANATOMICAL DATA

Oak wood as a type is easily recognized. The sapwood is creamy white to buff; the heartwood varies from light tan to dark brown, with or without a reddish cast. The wood ranges from typically ring porous to semi-ring porous, that is, with either an abrupt or gradual transition in size from the larger springwood vessels, arranged in a one to several-seriate zone, to the small summerwood pores (Figs. 1–4). The latter are radially aligned and

embedded in flame-shaped tracts of tissue, which, to the naked eye, appear light in color. At higher magnifications, this tissue is resolved into a mass of longitudinal parenchyma and vasicentric tracheids, similar in all respects to that sheathing the springwood vessels (Figs. 3, 4). The transverse section is further figured by concentric bands or metatracheal-zonate bands of parenchyma,[2] which at 10×, appear as fine white lines extending tan-

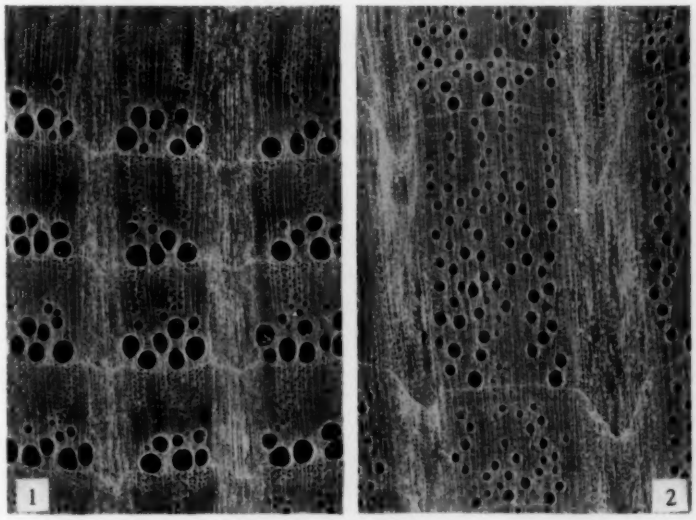

Fig. 1. *Q. bicolor* Willd. (9×) Illustrating the true ring porous type of oak wood. Note also the characteristic appearance of the thin-walled, angled summerwood pores of white oaks at low magnifications.

Fig. 2. *Q. virginiana geminata* Sarg. (9×) Illustrating the semi-ring porous type of oak wood common among the live oaks. Note the appearance of the thick-walled, rounded summerwood pores of the red oaks at low magnifications.

gentially throughout the summerwood. The wood rays are of two types, *a*, simple and uniseriate, and *b*, compound or aggregate and multiseriate (Figs. 5, 6). The multiseriate rays strikingly figure the various planes of section and are the most characteristic feature of oak wood. On the transverse section, as viewed with the naked eye, they are visible as more or less widely spaced, broad, light bands which stand out against the darker background of fibrous tissue; slight magnification reveals that the large rays are separated by numerous fine white lines, the uniseriate rays. In flat-sawn lumber, the large rays are staggered and vary in length along the grain from one-sixteenth to several inches. Quarter-sawn boards exhibit

[2] Short strands of longitudinal parenchyma more or less united tangentially into zones whose course runs irrespective of the pores.

conspicuous, extremely high ray flecks which are fairly widely spaced and form a figure not duplicated in any other native wood.

With special reference to the present problem of determining subgeneric limits, it has long been known that there are two sharply defined groups in the genus *Quercus*, distinct from one another on the basis of variations in the structure of the secondary xylem (1, 3, 16). Anatomists have recognized the close parallelism of these two groups to LEUCOBALANUS and

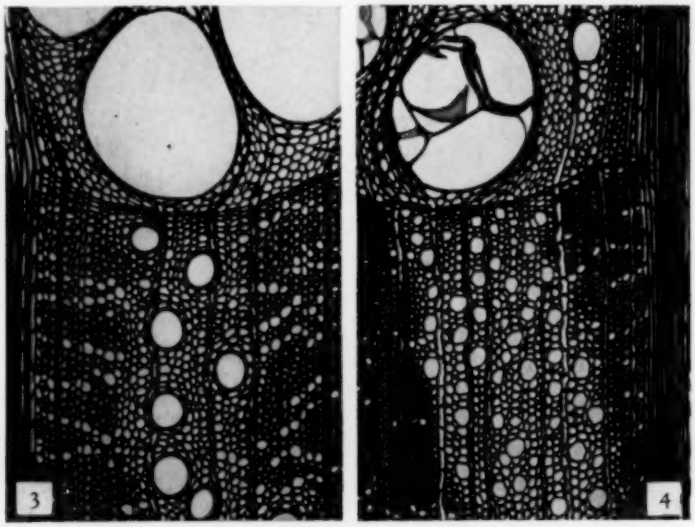

Fig. 3. *Q. coccinea* Muench. (60×) Showing the rounded, thick-walled summerwood pores of the red oaks at higher magnification. Note the absence of tyloses from the springwood vessels.

Fig. 4. *Q. alba* L. (60×) Showing the thin-walled, angled summerwood pores of the white oaks. Note the tyloses in the springwood pores.

ERYTHROBALANUS of systematic botanists, even though the latter have never used these features. The important rôle they play has now become apparent.

The structural and physical features of the wood of the anatomical subdivision of *Quercus* are tabulated below.

TABLE 2

Structural and physical characteristics of red and white oak wood

RED OAK TYPE CORRESPONDING TO ERYTHROBALANUS	WHITE OAK TYPE CORRESPONDING TO LEUCOBALANUS
1—Heartwood with reddish cast	1—Heartwood light tan to brown
2—Tyloses sparse in heartwood	2—Tylose abundant in heartwood
3—Summerwood pores rounded, thick-walled (3 to 8 microns, Figure 3)	3—Summerwood pores angled, thin-walled (less than 3 microns, Figure 4)

The first two of these overlap and can not be used with certainty. The third is apparently absolute. It seems reasonable to assume that this indication of group relationships is of equal or greater importance as compared to that signified by those features which have been utilized in the past (see Table 1), especially in view of the contradictory nature of these latter-mentioned criteria. This assumption gathers further strength from an analysis of the data covered in the succeeding paragraphs.

The division of *Quercus* species on the basis of wood anatomy closely conforms to that evolved from the criteria listed in Table 1, When the present study was initiated, no exceptions to this rule were known, or if known, had escaped critical attention. As the list of species studied has grown, however, so has the list of exceptions, until at the present time, after a comprehensive examination of some fifty "species" and "varieties", eight have been found, which, on the basis of this criterion (3 in Table 2), are at variance with the groupings accepted by taxonomists. Of extreme interest is the fact that all of these are placed by systematists in LEUCOBALANUS, no departures occurring among the red oaks. Furthermore, these are the only exceptions to the general rule that the white oaks should possess leaves devoid of bristle-tipped lobes or spiny teeth on the leaf margins. The "white oaks" exhibiting "red oak" wood are *Q. emoryi* Torr., *Q. dumosa* Nutt., *Q. virginiana* Mill., *Q. reticulata* H. B. K., *Q. arizonica* Sarg., *Q. oblongifolia* Torr., *Q. engelmanni* Greene, and *Q. douglasii* Hook. & Arn.

Considering now the problem of devising a classification permitting of the absolute segregation of *Quercus* species into red and white oak types, a means of separation must be found that will retain the natural units and at the same time permit of no exceptions to the rule. As little change as possible should be made in the existing classification in order to avoid confusion upon the adoption of the revised system. Analysis of the correlation between wood anatomy and leaf-form reveals a plausible change which is at once simple and satisfies every demand made upon it by systematic botany. The proposal is made that the two groups, ERYTHROBALANUS and LEUCOBALANUS be retained, but that they be redefined as follows:

Leucobalanus:	*Erythrobalanus:*
Summerwood pores angled, thin-walled; leaves devoid of spinose teeth or bristle-tipped lobes.[3]	Summerwood pores rounded, thick-walled; leaves wholly or in part with bristle-tipped lobes, apex apiculate, or margins with spiny teeth.

[3] Leaves may be coarsely sinuate-toothed, as in the "chestnut oaks," but the ends of the teeth are rounded, not spiny.

The value of the above definitions is at once evident, since they clearly define the natural groups, and are usable in the field and herbarium by expert and layman alike. Their adoption affects the position of the eight species listed above, and these only; these species should be transferred from LEUCOBALANUS to ERYTHROBALANUS.

It may be argued that the genus *Quercus* can be subdivided arbitrarily by the use of existing criteria without employing a new variable, wood anatomy. A distinct subdivision of species might be suggested based on any one feature listed in Table 1. Were only an artificial segregation of species the ultimate objective, this possibility is granted. If the principles of taxonomy are to be respected, however, a grouping, to be acceptable, must indicate the natural affinities that exist between species. The corollary follows, therefore, that the measure of such subdivisions must be indicative of these relationships, and it is obvious from the previous discussion that the features listed in Table 1 are inadequate for such a purpose. Further, if the subdivisions are to be workable, the basic criteria must always be present. Leaves and wood are invariably available for examination, both in the forest and in the herbarium, in the latter because it is customary to mount sprays of foliage on herbarium sheets, thus supplying sufficient wood (the twig) and leaves to permit of accurate diagnosis. This obviates the difficulties encountered in classification when only sterile material is available. No features exhibited by the oaks, other than those proposed, display such a positive correlation and are so easily recognized. None have such omnipresence. There are no exceptions to the rule.

THE EVIDENCE AGAINST ADDITIONAL SUGBENERA

This discussion cannot logically be concluded without considering the possibility of the creation of a third subgenus, this to include those controversial species which inherently present composite features present in both the red and white oaks. Critical examination of the eight species it is proposed to transfer from LEUCOBALANUS to ERYTHROBALANUS reveals that all have evergreen foliage (persistent until the second season) with the exception of *Q. douglasii*. The interpretation of the characteristic of persistent foliage is, in itself, intangible, but greater weight may be assigned to this feature when it is considered in conjunction with the fact that all of the evergreen oaks have wood of the red oak type. Thus, within the new boundaries of ERYTHROBALANUS proposed in this paper, there are fourteen species[4] which exhibit evergreen foliage. The question arises, there-

[4] *Q. emoryi* Torr., *Q. dumosa* Nutt., *Q. virginiana* Mill., *Q. arizonica* Sarg., *Q. reticulata* H. B. K., *Q. oblongifolia* Torr., *Q. engelmanni* Greene, *Q. agrifolia* Nee, *Q. vaccinifolia* Kell., *Q. wislizenii* A.DC., *Q. hypoleuca* Engel., *Q. myrtifolia* Willd., *Q. chrysolepis* Liebm., *Q. tomentella* Engel.

fore, as to whether or not this group is sufficiently distinct to warrant subgeneric rank.

The red and white oaks have been defined through the correlation that exists between leaf-form and specific features present in the summerwood. The other features now in common use diagnostically have been shown to be unsatisfactory, since they fail to denote accurately the natural affinities occurring in the genus. A third subgenus, were it to be assigned equal rank to LEUCOBALANUS and ERYTHROBALANUS, must show a similar correlation between leaf-form and wood anatomy. Furthermore, both leaf-form and wood structure, as exhibited by this third group, would have to be sufficiently different in character from those of the other groups to permit of ready recognition.

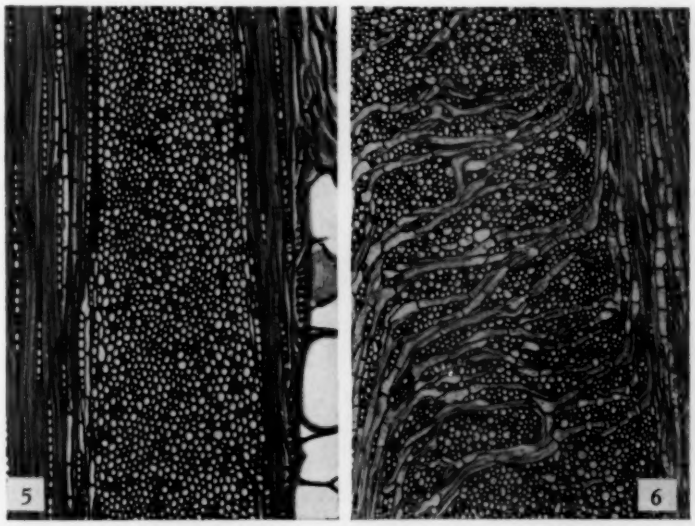

Fig. 5. *Q. stellata* Wang. (60×) Illustrating the true compound ray common to all oaks. Note the uniseriate rays.

Fig. 6. *Q. virginiana* Mill. (45×) Illustrating the aggregate ray type common only among the live oaks.

In leaf features alone, the evergreen oaks are certainly distinct. However, in attempting to correlate the anatomy of the wood with evergreen habit, sufficient variation is encountered to cast doubt upon the merit of this feature in assigning subgeneric rank. As a group, the species enumerated on this page tend to possess wood of the semi-ring porous type, in contrast to the ring porous condition present in the deciduous forms (Figs. 1–4); nevertheless, *Q. emoryi*, *Q. arizonica*, and *Q. myrtifolia* commonly possess ring porous wood. The tendency to form aggregate rays in

lieu of those of the compound type is found only in certain of these species. Scalariform perforation plates, an extremely rare feature of oak wood, are restricted to this group, yet this feature cannot be used, due both to the infrequency of its occurrence and to the fact that is evinced by but several of the species listed. Sclerosed tyloses are also present, but too sporadic to be significant. Springwood vessel diameters,[5] on the average, are smaller in these species than in the deciduous forms, but certain species in each group overlap sufficiently to nullify the mathematical significance of this character.

Within ERYTHROBALANUS the evergreen oaks form a small congeries which is so well defined that it cannot be ignored. This situation is not denied; nevertheless, these species, considered together, should not be accorded subgeneric rank on the basis of present evidence. Perhaps, with additional study, the group will attain greater distinctness as an entity. It is admitted that the evergreen oaks have many characters in common, and since they exhibit all of the xylary features accepted as primitive for the oaks (as well as certain other plant groups)[6] they deserve a significant niche in the phylogeny of the genus. The premise seems logical to designate this group as the "live oak" type within the subgenus ERYTHROBALANUS.

Comparable arguments may be advanced that no other aggregate of species within the newly defined LEUCO- and ERTHROBALANUS merits subgeneric rank, however distinct it may be on the basis of foliage alone. The so-called "chestnut oaks", admitted to be a definite segregate of LEUCOBALANUS, have anatomical features identical with the other white oaks. The Rubrae and Laurifoliae of Small (21) merge insensibly on the basis of wood anatomy. Nor do the Virginae of Small have any significance when the above mentioned facts are considered. Small's Albae are merely a southeastern extension of LEUCOBALANUS. For field identification Small's divisions may have intrinsic value, but as indicators of natural affinities they cannot be accepted.

In conclusion, it is conceded that the changes suggested in the classification of the oaks are tentative, pending such time when all the species embraced by LEUCOBALANUS and ERYTHROBALANUS can be critically examined. Certainly, wood anatomy promises to be a valuable tool in clarifying the confusion now prevailing in this genus. Further investigations are under way to determine whether variations in the anatomy of the secondary phloem will prove equally valuable in classification, and

[5] The tangential diameter of the pores is commonly used, as this is a more conservative measure than the radial axis.

[6] Tendency toward diffuse porous wood and aggregate rays, and scalariform perforation plates in the smaller summerwood vessels (2. 7 10, 23, 26).

whether these data will substantiate the deductions made in this paper on the basis of wood anatomy. Preliminary study has indicated that such will be the case; these results will be reported at a later date.

SUMMARY

The criteria used at present in delimiting LEUCOBALANUS and ERYTHROBALANUS in the genus *Quercus* do not provide for a satisfactory segregation of species according to their natural affinities.

Such flagrant exceptions occur that the logic of these criteria is questionable. No one feature now in common use in defining either of the two subgenera is not duplicated in the alternate subgenus.

Two types of wood structure are shown to exist within the genus *Quercus*, permitting of an absolute segregation of species.

The two groups defined on the basis of wood anatomy closely parallel LEUCOBALANUS and ERYTHROBALANUS as now recognized by systematists, with the exception of the following species: *Q. emoryi* Torr., *Q. dumosa* Nutt., *Q. virginiana* Mill., *Q. reticulata* H. B. K., *Q. arizonica* Sarg., *Q. oblongifolia* Torr., *Q. engelmanni* Greene, *Q. douglasii* Hook. & Arn.

The eight species listed above are the only exceptions to the rule that the leaves of the white oaks be devoid of bristle-tipped lobes or spiny teeth on the leaf margins.

An absolute correlation exists between leaf-form and the structure of the summerwood; those species having leaves, either wholly or in part, with bristle-tipped lobes or spiny teeth, all possess wood of the red oak type.

LEUCOBALANUS and ERYTHROBALANUS are redefined on the basis of this correlation. Pursuant to this new definition, the eight species listed above are transferred from LEUCOBALANUS to ERYTHROBALANUS.

All of the evergreen oaks have wood of the red oak type, and the feasibility of creating a third subgenus to include these species is indicated. The evidence being to the contrary, it is proposed to designate these species as the "live oak" type in ERYTHROBALANUS.

The wood of the evergreen oaks alone exhibits all of the anatomical features conceded as primitive for the oaks, namely, tendency toward semi-ring porous wood and aggregate rays, and scalariform perforation plates in the smaller summerwood vessels. These features are sporadic, however, and no one is common to all live oaks. There is no absolute correlation possible between evergreen habit and wood anatomy other than that stated above.

No subgroups within LEUCOBALANUS or ERYTHROBALANUS, as defined in this paper, merits subgeneric rank, however distinct in foliage.

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Pocomoke Swamp: A Study of a Cypress Swamp on the Eastern Shore of Maryland

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(WITH FIVE FIGURES)

INTRODUCTION

Though the Pocomoke River Swamp greatly resembles the Dismal Swamp in physical characteristics, little attention has been given it. The latter is usually regarded as the most northern of the extensive southern cypress swamps characteristic of the Atlantic Coastal Plain. Separated from the Dismal Swamp by Chesapeake Bay, the Pocomoke Swamp appears to be an isolated northern extension of the larger development on the mainland and offers an excellent opportunity for comparative study.

THE SWAMP AND ITS RELATION TO THE SURROUNDING TERRITORY

Once considered an almost impenetrable wilderness, the swamp was early exploited for its valuable timber. Consequently it has been lumbered over its entire extent. Much of its original area in the upper part is now drained and cultivated. However, because of the low elevation, parts of the swamp have not been drained and have seldom been entered since lumbering ceased many years ago. These areas, mostly along the tidal part of the river, are undoubtedly much like the original forest.

Pocomoke River, a tributary of Chesapeake Bay, has its source in lower Delaware, flows southward through southeastern Maryland and empties into Pocomoke Sound. The swamp at present occupies a narrow strip along each bank of the river and its tributaries. It is about 30 miles in length and varies from less than 0.5 to nearly 2 miles in width. The lower part of the river is brackish and is bordered with salt marsh which extends several miles upstream to where the swamp begins, about opposite the village of Rehobeth in Somerset County. Above Rehobeth the wooded swamp is continuous except where wide bends in the river bring it to the margin of the flood plain bordered by low, pine-wooded bluffs.

The only extensive areas of fresh water marsh occur at the mouth of Nassawango Creek and on a few river bends near Snow Hill. Otherwise emergent aquatics occur only as an extremely narrow strip along the river and mainly in its upper reaches. The portions of the swamp adjacent to the river are regularly flooded and drained by the tide which affects most of the river to above Snow Hill. Its average rise and fall is about 2.8 feet at Pocomoke City and 3 feet at Snow Hill. A few hundred yards from the river drainage at low tide is less complete and there is some standing water at all times. Even where ditches have been dug, the level contour, fallen

logs, cypress knees and accumulation of plant debris prevent much run-off at low tide. The land rises very gradually from the river and as it reaches an elevation above high tide it becomes less swampy with a gradual transition from swamp to upland forest. Occasionally there are more abrupt rises and the boundary of the swamp is then well marked.

The upper part of the river above the reach of the tide and in the neighborhood of the Maryland-Delaware line apparently was once bordered by a swamp of much larger extent than the narrow belt along the tidal portion of the stream. This region, however, has been more extensively lumbered and has been largely drained by deepening the channel of the river and by extensive ditching. Much of it is now in cultivation and possesses a characteristic black colored soil noticeable in the vicinity of Gumboro, Delaware. The original poor drainage resulted in an accumulation of peat of some depth. As a result of drainage, cutting and a severe drought in 1931, forest fire swept the whole area and burned persistently for about six months, locally destroying most of the peat accumulation and all the remaining forest. The conflagration was worst in an area now known as the Burned Swamp. Here the burning of the peat lowered the ground level so that an extensive area became covered with shallow water in spite of the drainage ditches. These have recently been deepened and much of the area at first covered with water is now dry causing consequent readjustments in the flora. There appear to be no cypress trees left in this vicinity and at present no trees of any kind grow along the most severe part of the burn. The parts where water is still standing are in the beginning of a hydrarch succession which should progress rapidly unless further disturbed by drainage.

The climate of the region is typically oceanic because of the ocean to the East and Chesapeake Bay to the West. Climatic data (Weeks, 1932) covering 21 to 26 years of record give for Pocomoke City a mean annual temperature of 57.3° F. July is the warmest month with a mean of 77.8° and February is the coldest with a mean of 36.6°. The average date of last killing frost in spring is April 14, and that of the first in the fall is October 29 giving a growing season of 198 days. Rainfall is well distributed throughout the year, being slightly greater during the growing season than in the winter, and averages 39.12 inches annually. Snowfall is light and seldom remains long on the ground, the average annual fall being 11 inches. The climatic conditions of the Dismal Swamp are very similar although, being to the south and on the mainland, the temperatures there are consistently a few degrees higher, the annual precipitation is several inches greater, and the growing period slightly longer (Kearney, 1901).

Worcester County, where most of the study was made, lies wholly within the coastal plain as does almost the entire peninsula, and is the only county in Maryland bordering on the Ocean. Its elevation varies from sea level to 51 feet above and averages about 35 feet (Perkins and Bacon, 1928). The total fall of Pocomoke River throughout the length of the county is slightly more than 30 feet which accounts for its sluggish flow and the presence of the swampy areas along it.

The soils have developed from gravel, sand, silt and clay transported by the Delaware, Susquehanna and Potomac Rivers from the Allegheny Ridges and deposited in coastal waters. They are mostly sandy loams or silt loams, porous enough to be well drained in spite of the low elevation (Perkins and Bacon, 1928). Soil in the swamp has no definite texture and if drained would be classified as muck or Portsmouth loam. The muck is usually underlain with the characteristic sandy subsoil of the region.

THE FLORA AND ITS ECOLOGICAL RELATIONSHIPS

Though climatic and physiographic conditions are much the same for all the region there are yet a number of varying factors, particularly edaphic, which limit certain species and communities to restricted areas. Saturated soil, alternate flooding and draining, standing water, accumulated organic material in varying quantities, sandy ridges, all contribute to the diversity of vegetation. Saturated soil and standing water are unfavorable to most plants because of poor aeration and an acid condition due to the accumulation of carbon dioxide (Kurz, 1928) and it has been shown by Bergman (1920) and others that under these conditions poor root growth results. Plants surviving must consequently have adaptations permitting root respiration or else, with limited root systems, be equipped with structures which maintain a slow rate of transpiration. The necessity for special leaf, stem or root modifications to meet the varying requirements of habitat limits the number of species appearing in any one place. The extensive literature on bog and swamp habitats treats these factors as well as wave action, ice, temperature and humidity, light and effects of drainage with varying degrees of emphasis (Rigg, 1916). Most of these factors are acting in the Pocomoke Swamp but, as elsewhere, not all are of equal importance in the distribution of the vegetation. The associations which occur must be explained by local conditions peculiar to this swamp and, although often overlapping and possessing many species in common, certain divisions on the basis of moisture and light conditions can be recognized. Communities which may be termed *Swamp Forest*, *Forest Stream Border*, *Fresh Water Marsh*, *Upland Border*, and

Burned Area will be discussed separately and in some cases further subdivisions made.

The nomenclature used for flowering plants is essentially that of Gray's Manual (seventh edition). The pteridophytes follow Bomquist (1934).

SWAMP FOREST

The swamp forest occupies the bulk of the area studied. Other communities discussed are, with the exception of the Burned Swamp, more or less marginal and of limited extent. The swamp is densely and evenly forested with a closed canopy producing heavy shade. Herbs and shrubs on the forest floor are limited in number. The soil is normally very wet or covered with shallow water in which sphagnum is abundant. The forested swamp might be divided into a tidal zone which is regularly inundated and drained, and a non-tidal zone, adjacent to the upland, with shallow water areas unaffected by the tide. However, with few exceptions the vegetation is uniform throughout and seems best regarded as a single community.

Trees

Cypress (*Taxodium distichum*) and swamp black gum (*Nyssa biflora*) are the dominant trees. They are mostly second growth with the exception of a few gnarled and misshapen specimens. In a typical stand the cypress ran from 13 to 24 inches in diameter breast high but were rather uniformly 80 years of age. Red maple (*Acer rubrum*) is equally abundant but occurs only infrequently in the dominant stratum. *Nyssa sylvatica* is a common associate and occasionally large specimens of sweet gum (*Liquidambar styraciflua*) are found near the upland border. Green ash (*Fraxinus pennsylvanica* var. *lanceolata*) is common throughout the swamp but is never very large. Small specimens of swamp cottonwood (*Populus heterophylla*) are occasionally noted. Within the swamp on slightly elevated ground are isolated specimens of loblolly pine (*Pinus taeda*) and pond pine (*Pinus serotina*), the latter being more abundant where standing water or poor drainage render the habitat more acid.

White cedar (*Chamaecyparis thyoides*) is scarce near the river but in the non-tidal portions of the swamp near the upland border it may become fairly abundant and form nearly pure stands. Such a tendency is noted throughout its range and in Virginia and North Carolina (Korstian and Brush, 1931) pure glades of white cedar have been found to occupy very acid soil and shallow peat underlain by sand. In Pocomoke Swamp the non-tidal portion with its standing water is more favorable to the formation of peat with its accompanying high acidity, and, where the white

cedar is most plentiful, the spongy peat accumulation has built up the soil level so that there is usually very little standing water. This condition seems more favorable to the establishment of white cedar than does the presence of deeper water.

Cypress is most abundant near the river's edge but seldom forms extensive pure stands except in shallow mill ponds on tributary streams (fig. 1) where the raising of the water level has excluded other species. Only a short distance from the river cypress decreases and black gum becomes increasingly more abundant so that over wide areas it is the most

Fig. 1. Open cypress stand in ponded stream. Note immense relic stump at left.

important tree. Especially where the water level may rise highest among the trees, the cypress, and to a lesser extent the gum, show characteristic swollen bases. Cypress knees are well developed and numerous, usually ranging up to about 2 feet in height. Since this is the depth of average tidal flooding it conforms with the contention of Kurz and Demaree (1934) that knees grow only to the level of average high water. In well-drained soil they are never present. At the river shore these knees form almost solid walls around the trunks next to the stream (fig. 2).

A frequent understory tree is the sweet bay (*Magnolia virginiana*), which is everywhere abundant in the swamp. Specimens of holly (*Ilex opaca*) and red cedar (*Juniperus virginiana*) are scattered throughout but are more abundant where the soil is least saturated. The margins of small streams and the river shore support numerous specimens of fringe tree

(*Chionanthus virginica*), blue beech (*Carpinus carolinana*), black alder (*Alnus rugosa*), and many viburnums of nearly tree size.

Vines

Many lianas drape the trees and occasionally reach their tops. Most noticeable are *Vitis* spp., *Bignonia capreolata*, *Smilax laurifolia*, *S. Walteri*,

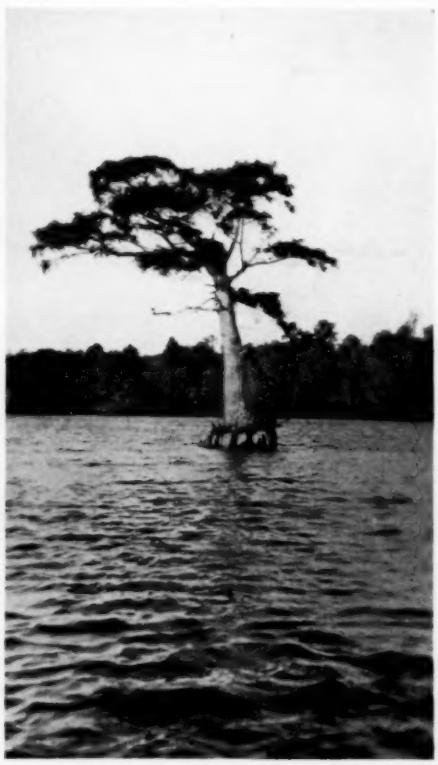

Fig. 2. Typical stream-margin habit of cypress with knees closely clustered at base.

Fig. 3. Isolated cypress characteristic of shallows in the river.

Tecoma radicans, *Rhus toxicodendron*, *Psedera quinquefolia*, and *Lonicera japonica*. *Bignonia capreolata* and *Smilax laurifolia*, both evergreen, are here near their northern limit, as is the muscadine grape (*Vitis rotundifolia*). Also occasionally found on trees are two interesting plants of southern range, the epiphytic gray polypody (*Polypodium polypodioides*) growing high on limbs of black gum and the parasitic mistletoe (*Phorandendron flavescens*) usually found on limbs of gum and maple. *Dioscorea glauca*,

Apios tuberosa, and *Mikania scandens* often overrun the lower bushes which may also be infested with love vine (*Cuscuta compacta*).

Shrubs

The shrubby growth, while not profuse or rich in species, contributes much to the beauty of the swamp. Although ranging through all parts, most species are more abundant in places where the shade is least dense and some, such as the viburnums, are mostly present near the swamp border along open streams. Ericaceous shrubs are plentiful and include *Rhododendron nudiflorum*, *Leucothoë racemosa* and several species of vaccinium, producing their flowers in early spring, while *Rhododendron viscosum*, *Lyonia ligustrina* and *Clethra alnifolia* blossom in the summer. Numerous and conspicuous in late spring and early summer are *Viburnum dentatum*, *V. nudum*, *V. cassinoides*, *V. prunifolium*, *Cornus amomum* and *Itea virginica*. *Decodon verticillatus* and *Cephalanthus occidentalis* flower in late summer, the former being common throughout the swamp forest. Not as numerous, but noticeable in fall and winter with their bright red fruits, are *Ilex verticillata*, *Pyrus arbutifolia*, *Benzoin aestivale* and *Evonymus americanus*. Occasionally along the river and very abundant near its mouth are large bushes of *Baccharis halimifolia*.

Herbs

Where the tide periodically floods the ground, especially in the dense shade of the forest, the number of species of herbaceous plants is not large. Very noticeable, however, are the ferns, *Osmunda cinnamomea*, *O. regalis* and *Lorinseria areolata* being most frequent. *Glyceria obtusa*, *Carex intumescens*, *C. lupulina*, and *C. folliculata* grow in scattered clumps, the extensive areas between being thinly populated with *Polygonum hydropiperoides*. *Polygonum arifolium* and *P. sagittatum* sometimes grow here in tangled masses. Other conspicuous herbs are *Impatiens biflora*, *Thalictrum polygamum*, *Rudbeckia laciniata*, *Bidens comosa*, *B. discoides* and several species of *Aster*.

Deeper in the swamp, where the tide has little effect and the water seldom is of much depth, are a wider variety of herbs. Those mentioned above are present, with the addition of clumps of *Carex debilis*, *C. crinita*, *C. serosa*, *Cinna arundinacea*, *Leersea virginica*, and *Rynchospora corniculata*. Covering the mud between these, the lizard's tail (*Saururus cernuus*) is by far the most abundant herb. Usually as isolated specimens and widely scattered, are *Boehmeria cylindrica*, *Ludvigia alternifolia*, *Lycopus rubellus*, *Eclipta alba* and the attractively flowered *Gentiana latifolia*, *Chelone glabra* and *Asclepias incarnata* var. *pulchra*. Throughout the entire

swamp forest are scattered, though frequent, specimens of the umbellifer, *Oxypolis rigidior* var. *longifolia*.

Rarely, near where bog iron ore was dug, are found small pools of deeper water in which grow *Potamogeton pulcher* and *Peltandra virginica*. Decayed stumps, logs and raised tussocks in this area are usually covered with *Mitchella repens*, *Trillium sessile*, *Anemone quinquefolia*, *Viola cucullata*, *Habenaria clavellata*, *H. cristata* and the fern *Athyrium acrostichoides*.

FOREST STREAM BORDER

Throughout most of the length of the river there is no marsh between the swamp and the water, and this is likewise true of all the tributary streams except in a few small areas at the mouths of some of them. This is probably accounted for by the strong tidal movement in most cases, and the narrow, deep channels with the consequent lack of sedimentation providing no new areas for invasion by marsh plants. The swamp forest represents an edaphic climax which has replaced most marsh land and has now become quite stable. The cypress trees extend to the water's edge (fig. 2) and, at rare places where there are shoals, may be found some distance out in the river (fig. 3). Hence most of the species characteristic of the tidal swamp forest are present along the stream borders, but there are a number much more abundant here than further in, and some additional ones make their appearance.

Extending a short distance out from the shore to the channel is a gently sloping shallow area of soft mud which is partly exposed at extreme low tide. From near Pocomoke City to Snow Hill, and probably as far as tide water reaches up the river, this strip is marked by a narrow zone of *Nymphaea advena*, growing from near the bank to just beyond the low tide mark. Nymphaea disappears below Pocomoke City, probably due to slight salinity at high tide in dry seasons.

It is interesing to note here the resistance of cypress to this occasional salinity. During an unusually dry season in the fall of 1930 the river water at Pocomoke City had a distinctly salty taste and fish characteristic of salt water were caught from the bridge there. *Nymphaea advena* showed considerable injury at this time, as did also a number of other plants at the water's edge, but the cypress showed no ill effects. Tides lower than usual prevented the salt water penetrating back into the swamp but some cypress were completely surrounded by it for several weeks. Some distance below the point where salt marsh appears there are a few old cypress trees near Cedar Hall growing at the river's edge but along a bank rising some distance above the water so that seepage of fresh water from the shore may explain their ability to survive there.

Orontium aquaticum and *Pontederia cordata* are often found next to the shore, within the zone of *Nymphaea advena*. Where the bank is slightly higher but still swampy, *Cicuta maculata*, *Sium cicutaefolium*, *Lobelia cardinalis*, *Aster* spp., and *Iris versicolor* are rarely present in addition to some species already mentioned in the swamp forest flora. On sandy spots, just at the high water mark, *Hydrocotyle umbellata* is sometimes found.

Species already named as members of the swamp forest but found in greater abundance overhanging the banks of streams are fringe tree, blue beech, black alder and rarely black willow (*Salix nigra*). Nearly all the shrubs of the swamp are in greater abundance here, *Viburnum* spp., *Vaccinium* spp., and *Rhododendron nudiflorum* all being conspicuous at flowering time. Also here the swamp rose (*Rosa carolina*) is noteworthy and in some places forms dense tangles. There is little of the herbaceous swamp flora present along the immediate margin of streams. Probably this is accounted for by water action and the lower soil level where the mud has been washed out between the trees and larger shrubs in a series of hollows all along the shore line. Vines are more in evidence as seen from the water for light conditions are far better than in the interior of the forest.

FRESH WATER MARSH

Areas which may be termed marsh are rarely present within the swamp limits. Along the lower part of the river, however, the swamp is entirely replaced by extensive areas of marsh. These might be classed as fresh, but contain numerous species characteristic of brackish water and many fresh water species are excluded. There is a gradual transition into salt marshes near the river's mouth. Since this marsh is so radically different and so sharply delimited from the swamp proper it will not be treated further here.

Only at the mouth of a few streams, locally in the upper river, and along tributaries, are there limited areas of fresh water marsh having a close relationship to the swamp. The soil in these marshy areas seems to have become recently available to emergent species. Apparently it was built up from silt deposited by the retarded current. A few marshy areas on tributaries of the river seem to have resulted from the draining of old ponds. These are partly invaded by shrubs and a few trees but changes in their outline and composition do not seem to be rapid.

Nearest the water, *Nymphaea advena* again forms the outer lines of vegetation and back of it *Pontederia cordata*, *Sagittaria latifolia*, *Peltandra virginica* and *Orontium aquaticum* are most abundant. Further within the marsh *Typha latifolia* is common and may form scattered dense stands. *Phragmites communis* is also found in pure stands at the mouth of Nas-

sawango Creek but is rare elsewhere. Other species are found scattered over the marsh in separate patches or are intermingled. Conspicuous among these are *Dulichium arundinaceum, Rynchospora macrostachya, Carex stipata, Trisetum pennsylvanicum, Elymus virginicus, Zizania aquatica* and occasional clumps of *Hibiscus* spp. Many species of carex, juncus and others of smaller stature are present, and where marsh merges with swamp the species named in the preceding section appear. Where shrubs enter the inner area, *Rosa carolina* and species of rubus are important. In the fall the marshes become bright with the blossoms of *Helenium autumnale, Bidens trichosperma, Aster paniculatus* and a few others. Although periodically flooded with the tide, the marshes are well drained at low tide and apparently differ little from those which do not border swamp land. Only in ponds beyond the influence of the tide is the deeper water sometimes covered with the floating leaves and blossoms of the water lily (*Castalia odorata*).

UPLAND BORDER

By upland border is meant the area of transition from swamp to upland and not the upland forest itself. The change may be abrupt or a gradual one with considerable mingling of species. This depends on whether the land rises abruptly or with very gentle slope and hence both narrow and broad transition zones may be found. The gradual change is usual where small lateral streams of short extent diverge and lose their identity, and the abrupt change is more often found along a stream where there is a narrow belt of swamp not intercepted by lateral branches. Also within the swamp are occasional raised sandy areas or islands which are not flooded with water and are quite dry at the surface though possessing a constantly high water table. These support a flora similar to that of the upland border.

Trees

The tendency of white cedar to become more abundant near the upland and sometimes form nearly pure stands has already been noted. This tree is characteristic of the transition zone but seems to do best just within the swamp where the forest floor has been built up above the water level by peat accumulation. Such a condition is more often found where the transition from swamp to upland is gradual. Along the upland border where the soil is less peaty are found a number of oaks, chiefly water oak (*Quercus nigra*), willow oak (*Q. phellos*), swamp chestnut oak (*Q. michauxii*) and white oak (*Q. alba*). Other broadleaved species, notably tulip poplar (*Liriodendron tulipifera*), river birch (*Betula nigra*) and beech (*Fagus grandifolia*) occur here, and at scattered points most species of the

upland forest may be found. Where the ground is mostly above swamp level, however, loblolly pine becomes the most abundant tree. In the upland it forms the extensive pine forests which are characteristic of this region and nearly everywhere surround the swamp. Virginia pine (*Pinus virginiana*) and short-leaf (*P. echinata*) are common only where the soil is definitely dry and sandy, although such areas may occur adjacent to the swamp on the more abrupt rises.

Shrubs

Probably the most notable characteristic of this transition zone is the abundance of evergreen shrubs which sometimes form dense thickets. Although numerous in individuals, the species are few and consist almost entirely of *Kalmia latifolia*, *Ilex glabra*, *Myrica cerifera*, and occasionally small trees of *Ilex opaca*. The first two frequently attain large size. On the ground are often found such small evergreens as *Mitchella repens*, *Gaultheria procumbens*, *Lycopodium complanatum*, and more rarely *Selaginella apoda*. Nearly all of these evergreens are also components of the upland forest but their greater abundance here must in some way be related to the presence of the swamp.

The most likely explanation of this preponderance of evergreen shrubs must lie in the fact that the lower levels of soil are permeated with the acid, oxygen-depleted swamp water. In this zone the underlying sandy layers are above the swamp level and the surface is not covered with the mud of the swamp, but is sandy and porous with little accumulation of peat. Although it is poorly drained because of the high water table, water normally never stands over it but sinks rapidly and drains off to the level of the swamp. Because of the slight elevation above the swamp, only a shallow surface layer of soil permits air to penetrate freely for the deeper layers remain saturated with water. This makes a habitat of very limited extent greatly resembling that described for the evergreen shrub bogs of North Carolina (Wells, 1932). The comparatively dry surface and fluctuating water table must exclude many swamp or marsh species. Other species are probably unable to develop a normal root growth since the oxygen deficiency of the soil water may render the habitat physiologically dry though possessing a high water table. Here the thick, waxy-coated leaf structure of the xerophytic evergreens should check transpiration and enable them to succeed much better than the thin leaved deciduous species whose usual widespread root development would be greatly retarded. Higher in the upland, the deciduous species with their rapid growth offer serious competition to the slowly growing evergreens. The lower winter temperatures in Maryland, and the isolation of this swamp

from those farther south, exclude from it the wealth of species found in the southern evergreen shrub bogs.

Although evergreen shrubs are most abundant, this border zone also contains scattered specimens of other shrubs characteristic of the swamp and a few which are more often found here than elsewhere. Of common occurrence are *Vaccinium* spp., *Rhus copallina*, *Amelanchier oblongifolia*, and where not too shaded, *Sambucus canadensis*. Several species of Smilax are abundant in places and with the thick growth of shrubs often make this border region more difficult to penetrate than any other part of the swamp.

Herbs

Where the upland border is densely shaded by trees and shrubs there are few herbaceous species. A scattering of those common to the swamp occur here and in addition *Arisaema triphyllum*, *Genetiana Saponaria*, rarely *Lilium superbum* and others less conspicuous may be found. *Asplenium platyneuron*, *Botrychium virginianum*, *Dryopteris intermedia*, *D. noveboracense*, *Athyrium asplenioides*, *A. thelypteroides* and, where quite dry, *Pteridium latiusculum* here offer a variety of ferns in addition to those of the swamp although none are plentiful except the last named, and that only in the drier parts.

The herbaceous vegetation of the more open parts of the upland swamp border is much more abundant both in individuals and species. This is especially true along roadsides entering the swamp. Only the characteristic plants will be mentioned. In rather wet semi-open situations are *Vernonia noveboracensis*, *Mimulus alatus*, *M. ringens*, *Gerardia purpurea*, *Ruellia ciliosa*, *Houstonia caerulea*, *Viola* spp. and many others. Less conspicuous are *Diodia virginiana*, *D. teres*, *Penthorum sedoides*, *Ludvigia palustris*, *Onoclea sensibilis*, *Dryopteris thelypteris*, *Eleocharis obtusa*, *Juncus setaceous*, *Rynchospora glomerata* and *Carex* spp.

BURNED AREA

The sections of the swamp that have already been described lie mostly along the length of the river and its larger tributaries in Worcester County. The upper part of the river near the southern border of Sussex County, Delaware, seems to have once been occupied by a swamp of considerable extent. This was somewhat different from that along the lower river in that it was entirely above tidewater and possessed a much deeper accumulation of peat. The timber and most of the peat have recently been destroyed by fire so that the region now is quite changed from its original condition and is undergoing successions which would justify further observation.

Due to the accumulation of peat, the fire which swept the area burned most persistently near the center of the swamp. At present this area has

Fig. 4. Burned swamp. Here the peat completely burned out and hydrarch succession was initiated.

Fig. 5. Lightly burned swamp. Secondary succession beginning with shrubs and sucker sprouts.

practically no accumulation of peat and the lower parts are covered in places with open water several feet deep (fig. 4). The bottom is hard and no plants have yet become established in the deepest spots although *Typha*

latifolia is present in clumps on the shallower areas and occasionally the Virginia chain fern (*Anchistea virginica*) and mermaid weed (*Proserpinaca palustris*) are present. On fallen logs and stumps *Rhexia virginica*, *Solidago fistulosa* and a few clumps of grass have at times obtained a temporary foothold.

Away from the center the water is shallower and here over a large area *Typha latifolia* has thoroughly established itself practically to the exclusion of any other species. Bordering this is an irregular region where the ground may be above the water level and again may be covered with standing water a foot or more in depth. Where the water is from a few inches to a foot deep *Anchistea virginica* and *Proserpinaca palustris* are usually the most abundant species although there are areas where *Typha latifolia* again forms dense stands. There are other herbaceous plants scattered in the deeper water but these are of more common occurrence in water only a few inches or less in depth. Conspicuously flowered herbs are *Rhexia virginica*, *R. aristosa*, *R. mariana*, *Mimulus ringens*, *Aster novi-belgii*, *Hypericum virginicum* and *Solidago tenuifolia*. In the same area *Scirpus pedicellatus* and *Juncus effusus* are both very abundant and commonly found are *Lorinseria areolata*, *Eleocharis tuberculosa*, *Juncus acuminatus*, *Carex lurida*, *Rynchospora microcephala*, *Ludvigia sphaerocarpa*, *L. alternifolia*, *Polygonum setaceum*, *P. pennsylvanicum*, *Pluchea foetida*, and cotton grass (*Eriophorum virginicum*). Bordering the water and especially along ditches by the roadside *Eupatorium purpureum*, *E. verbenaefolium*, *Vernonia noveboracensis*, *Erianthus saccharoides* and occasionally *Epilobium angustifolium* are conspicuous in late summer and fall. Sphagnum is here very abundant in shallow water along the margin and the dense mats of polytrichum on the marginal soil deserve mention. In wet soil near the borders of the water-covered areas are often found *Habenaria lacera*, *Spiranthes cernua*, *Xyris caroliniana*, and less frequently *Bartonia virginica*. On most of the raised areas of soil and especially along the roadside banks, *Spirea tomentosa* is the most abundant small shrub and with it as well as on stumps and tussocks *Solidago fistulosa* is conspicuous.

Bordering the area where fire destroyed all trees are extensive tracts where the peat has only occasionally burned to the subsoil and where a few scattered loblolly pines survived and are producing some seedlings. Here most of the water has been drained away. The ground is covered with sphagnum and polytrichum, while scattered everywhere *Juncus marginatus*, *Juncus effusus*, clumps of *Scirpus pedicellatus*, *Anchistea virginica*, and species of Ludvigia are the most abundant herbs. A shrubby growth is filling in the higher parts (fig. 5). Most common on these raised

areas are *Myrica cerifera*, *Itea virginica*, *Clethra alnifolia*, *Decodon verticillatus* and seedlings of red maple, sweet gum, loblolly pine, black gum, black willow and swamp cottonwood. Red maple seedlings are the most frequent of the forest tree species invading the area at present. Of smaller stature than these are species of Vaccinium and Rubus while beneath them *Lycopodium alopecuroides* is especially abundant.

PHYTOGEOGRAPHIC CONSIDERATIONS

Adams' (1902) suggestion that the present distribution of plants in the eastern half of the United States has resulted from a northward dispersal from the southeastern states since the recent era of glaciation has much evidence to support it. In the northern bogs many glacial marginal species have been retained as relicts of the time when the great ice sheet covered the northern United States and Canada (Dachnowski, 1911; Bird, 1923). Studies of wind borne pollen preserved in peat (Fuller, 1929; Sears, 1932), and the stratification of such peat deposits (Dachnowski, 1921) give evidence of climatic changes which occurred in the past. Since the great ice sheet receded there have probably been several major climatic fluctuations and evidence in general seems to indicate that for this region there is a trend to a warmer and drier period. The present distribution of bog and swamp plant societies (Transeau, 1903; Gates, 1911) indicates that the flora of bogs is a relict of past climatic conditions and in the south is being replaced by species characteristic of the present normal hydrophytic vegetation of swamps. If these facts are true, a comparison of the flora of Pocomoke Swamp to that of similar areas to the North and South might give some evidence of the extent here of this northward migration of southern species.

The tidal portions of the swamp forest are relatively stable and probably much like the original plant covering before the commencement of man's extensive lumbering activities. In the driest seasons the water level remains nearly the same and abnormally high tides caused by wind may still flood the innermost parts. Physical conditions have remained practically unchanged and fire has seldom entered. It is probable that selective lumbering of cypress and more recently of gum and other species has changed the proportion of valuable trees to inferior species but qualitatively it must be much the same. Most of the second growth is now rather old, showing the dominants, subdominants and understory growth of a mature community.

Upon comparison with other similar areas which have been described, this swamp, though possessing an acid soil and much sphagnum with

associated bog plants, still is quite different in dominant trees and associated species from the northern bogs of glaciated regions. However, it probably contains more plants which are of boreal relationship than does the pine forest of the South Atlantic coastal plain which surrounds it. Many of the species found here also occur in swamps much farther north and south, but those peculiar to bogs are mainly absent and the presence of *Taxodium distichum* and *Nyssa biflora*, as the dominant trees, gives an aspect like that of southern swamps. The region is largely cut off from the South and West by Chesapeake Bay and from the northern extension of the coastal plain by Delaware Bay. Though species common in the pine barrens occur on the raised sandy areas within the swamp, yet they do not form the characteristic associations of the barrens, and neither the New Jersey nor southern type of pine barren can be said to exist here. This has been explained as due not to climate but to the comparative immunity to fire which Chesapeake Bay with its many waterways intersecting the land has given the region (Lutz, 1934).

Most of the species collected in Pocomoke Swamp are also found in the Dismal Swamp (Kearney, 1901) and again many of the most common plants are also abundant in the Okefinokee Swamp of southern Georgia (Wright and Wright, 1932). The dominant trees, most abundant associates and understory plants are identical with those of the Dismal Swamp region as are also the zones along streams and the girdles of included open areas. Both lack an abundance of flowering plants in the densely shaded and flooded areas dominated by gum, cypress, and maple. It differs mainly from the Dismal Swamp in having fewer species of the evergreen shrubs developed so extensively in pocosins farther south. Most noticeable as common to the Dismal Swamp but absent from the Pocomoke Swamp are the growths of cane (*Arundinaria tecta*). This species has been collected in Maryland near Annapolis, considerably north of the Pocomoke region, but it has not been found in this swamp and probably has been prevented by Chesapeake Bay from migrating here.

From these generalizations it would seem that Pocomoke Swamp vegetation is more closely related to that of swamps farther south than to any vegetation northward. The dominants are largely southern species as are numerous conspicuous shrubs and herbs. The whole appearance is that of swamps much farther south but the presence of northern species leads to a question of just how numerous and important these may be.

In an attempt to show more clearly the relationships of the flora, the species collected have been distinguished on the basis of their ranges. Those species whose range lies largely to the north of the swamp are desig-

nated by N, and S indicates those which largely range southward. The ranges are admittedly generalized, having been determined largely from the available manuals. In general, those typically southern species which range north of the swamp but are restricted to the Coastal Plain have been considered as of southern affinity.

Obviously the numerous species of common occurrence from Canada to Florida have no bearing on the problem. These are unmarked. They comprise 57 per cent of the swamp flora (159 species). Of the species ranging largely northward there are 9, only 3.2 per cent of the total flora while 40 per cent or 111 species range largely southward. Of the 9 northern species, 7 are here near the southern limit of their ranges while only 36 per cent of the southern species here approach their northern limits. The swamp then provides conditions far more favorable to southern species and its flora is predominantly of southern affinity. The list of plants collected by Kearney in the Dismal Swamp area includes only one of the northern species (*Carex canescens*) found in Pocomoke Swamp and indicates a flora there far richer in southern species.

It seems then that the edaphic and climatic conditions of Pocomoke Swamp must be similar to those of swamps farther south. The oceanic climate, fluctuating tide, poor drainage and consequent poor aeration combine to restrict the flora and southern swamp species are best adapted to the extremes of this complex which requires special means of transpiration control and tolerance to poorly aerated saturated soil.

Compared with the Dismal Swamp flora there is a much reduced number of southern swamp species and in addition 36 per cent of these species are approaching the limits of their ranges. These facts indicate that Pocomoke Swamp is either an outlier or very near the northern fringe of the center of maximum development of the typical southern swamp.

SUMMARY AND CONCLUSIONS

The Pocomoke Swamp on the eastern shore of Maryland is of particular botanical interest because it is probably the most northern extensive area of its kind. The factors effective in maintaining the habitat and consequently the vegetation seem entirely comparable to conditions controlling the larger swamps to the south.

The swamp flora, being little disturbed by man, offers an excellent opportunity for obtaining indicators of the present edaphic, biotic, and climatic conditions of the region and at the same time a basis for comparison with the flora of other regions.

The forest is dominated by cypress, swamp black gum, and red maple

and possesses a limited growth of associated shrubs and herbs because of poor light and drainage. The greatest variation among the dominants, and associates as well, is definitely related to tide and drainage. The moisture factor results in nearly pure stands of white cedar near the upland borders and at the opposite extreme almost pure stands of cypress along the more deeply flooded river margins.

The transition from swamp to upland has the greatest variety in species of shrubs and herbs. The abundance of evergreen shrubs here indicates the xeric nature of the habitat and shows resemblances to the pocosins of the South. The open, raised, sandy areas within and bordering the swamp are characterized by numerous pine-barren species.

Parts of the upper swamp have been so devastated by fire that all plant life was destroyed. Many so-called "fire weeds" have invaded the area with other species and although retarded by fluctuating water levels these pioneer communities have initiated a hydrarch succession which should be interesting to follow in the future.

The flora of Pocomoke Swamp is more closely related to that of southern swamps than northern bogs. The preponderance of southern species bears out evidence that in the recent past, migration has been progressing from the southeastern United States. There are no indications that there will be any marked change in the swamp flora in the immediate future; it appears that it will remain essentially stable if left undisturbed.

LIST OF SPECIES COLLECTED[1]

PTERIDOPHYTA

OPHIOGLOSSACEAE

Botrychium obliquum Muhl.
Botrychium virginianum (L.) Sw.

OSMUNDACEAE

Osmunda regalis L.
Osmunda cinnamomea L.

POLYPODIACEAE

Pteridium latiusculum (Desv.) Hieron.
Dryopteris noveboracensis (L.) A. Gray
Dryopteris thelypteris (L.) A. Gray
Dryopteris intermedia (Muhl.) A. Gray
Polystichum acrostichoides (Michx.) Schott
Polypodium polypodioides (L.) Hitchc. S
Athyrium thelypteroides (Michx.) Diels.
Athyrium asplenioides (Michx.) Desv. S
Asplenium platyneuron (L.) Oakes
Onoclea sensibilis L.
Anchistea virginica (L.) Presl.
Lorinseria aerolata (L.) Presl.

EQUISETACEAE

Equisetum arvense L.

LYCOPODIACEAE

Lycopodium alopecuroides L. S
Lycopodium complanatum L. var. *flabelliforme* Fernald

SELAGINELLACEAE

Selaginella apoda (L.) Fernald

[1] Nomenclature essentially that of Gray's Manual (7th edition) except for Pteridophytes which are named as in Blomquist (1934).

Species ranging largely north of the swamp are marked N, south ranging species S, species of general distribution are unmarked.

SPERMATOPHYTA

GYMNOSPERMAE

PINACEAE

Pinus taeda L. S
Pinus serotina Michx. S
Pinus virginiana Mill. S
Pinus echinata Mill. S
Taxodium distichum (L.) Richard S
Taxodium ascendens Brongn. S
Chamaecyparis thyoides (L.) BSP. S
Juniperus virginiana L.

ANGIOSPERMAE

Monocotyledoneae

TYPHACEAE

Typha latifolia L.
Typha angustifolia L.

NAJADACEAE

Potamogeton pulcher Tuckerm.

ALISMACEAE

Sagittaria latifolia Willd.

GRAMINEAE

Erianthus saccharoides Michx. S
Paspalum laeve Michx. S
Echinochloa crusgalli (L.) Beauv.
Zizania aquatica L.
Leersia virginica Willd.
Cinna arundinacea L.
Trisetum pennsylvanicum (L.) Beauv. S
Phragmites communis Trin.
Glyceria obtusa (Muhl.) Trin.
Elymus virginicus L. var. *glabriflorus* (Vasey) Bush.

CYPERACEAE

Cyperus rivularis Kunth.
Dulichium arundinaceum (L.) Britton
Eleocharis obtusa (Willd.) Schultes.
Eleocharis tuberculosa (Michx.) R. & S. S
Fimbristylis autumnalis (L.) R. & S. S
Scirpus olneyi Gray
Scirpus lineatus Michx.
Scirpus pedicellatus Fernald. N
Eriophorum virginicum L.
Rynchospora corniculata (Lam.) Gray. S
Rynchospora macrostachya Torr.
Rynchospora axillaris (Lam.) Britton var. *microcephala* Britton S
Rynchospora glomerata (L.) Vahl. S
Carex foenea Willd. N
Carex seorsa E. C. Howe N
Carex canescens L. N
Carex stipata Muhl.
Carex crinita Lam.
Carex stricta Lam.
Carex debilis Michx. S
Carex lurida Wahlenb.
Carex lupulina Muhl.
Carex lupulina var. *pedunculata* Dewey
Carex intumescens Rudge S
Carex folliculata L. N
Carex vesicaria L. N

ARACEAE

Arisaema triphyllum (L.) Schott.
Peltandra virginica (L.) Kunth.
Orontium aquaticum L. S

XYRIDACEAE

Xyris caroliniana Walt.

COMMELINACEAE

Commelina hirtella Vahl. S

PONTEDERIACEAE

Pontederia cordata L.

JUNCACEAE

Juncus setaceus Rostk. S
Juncus effusus L.
Juncus canadensis J. Gay
Juncus acuminatus Michx.
Juncus marginatus Rostk.
Juncus aristulatus Michx. S

LILIACEAE

Oakesia sessilifolia (L.) Wats.
Lilium superbum L.
Trillium sessile L. S
Smilax tamnifolia Michx. S
Smilax walteri Pursh. S
Smilax rotundifolia L.
Smilax hispida Muhl.
Smilax lanceolata L. S
Smilax laurifolia L. S

DIOSCOREACEAE

Dioscorea glauca L. S

IRIDACEAE

Iris versicolor L.
Sisyrinchium gramineum Curtis

ORCHIDACEAE

Cypripedium acaule Ait.
Habenaria clavellata (Michx.) Spreng.
Habenaria cristata (Michx.) R. Br. S

Habenaria lacera (Michx.) R. Br.
Spiranthes gracilis (Bigel.) Beck.
Spiranthes cernua (L.) Richard.

Dicotyledoneae

PIPERACEAE

Saururus cernuus L. S

SALICACEAE

Salix nigra Marsh.
Populus heterophylla L. S

MYRICACEAE

Myrica cerifera L. S
Myrica carolinensis Mill.

BETULACEAE

Carpinus caroliniana Walt.
Betula nigra L. S
Alnus rugosa (Du Roi) Spreng.

FAGACEAE

Fagus grandifolia Ehrh.
Quercus michauxii Nutt. S
Quercus nigra L. S
Quercus phellos L. S
Quercus alba L.
Quercus rubra L. S
Quercus stellata Wang.
Quercus bicolor Willd.

URTICACEAE

Urtica procera Willd.
Boehmeria cylindrica (L.) Sw.

LORANTHACEAE

Phoradendron flavescens (Pursh.) Nutt. S

POLYGONACEAE

Polygonum pennsylvanicum L.
Polygonum setaceum Baldw. S
Polygonum hydropiperoides Michx.
Polygonum virginianum L.
Polygonum arifolium L.
Polygonum sagittatum L.

PHYTOLACCACEAE

Phytolacca decandra L.

CARYOPHYLLACEAE

Silene pennsylvanica Michx.

NYMPHAEACEAE

Nymphaea advena Ait. S
Castalia odorata (Ait.) Woodville & Wood.

RANUNCULACEAE

Thalictrum polygamum Muhl.
Anemone quinquefolia L.

MAGNOLIACEAE

Magnolia virginiana L. S
Liriodendron tulipifera L. S

LAURACEAE

Benzoin aestivale (L.) Nees

CRASSULACEAE

Penthorum sedoides L.

SAXIFRAGACEAE

Itea virginica L. S

HAMAMELIDACEAE

Hamamelis virginiana L.
Liquidambar styraciflua L. S

PLATANACEAE

Platanus occidentalis L.

ROSACEAE

Spiraea tomentosa L.
Pyrus arbutifolia (L.) L. f.
Amelanchier oblongifolia (T. & G.) Roem.
Rosa carolina L.

LEGUMINOSAE

Cassia marilandica L.
Cassia chamaecrista L. S
Apios tuberosa Moench.
Strophostyles umbellata (Muhl.) Britton S

LINACEAE

Linum virginianum L.

POLYGALACEAE

Polygala mariana Mill. S

ANACARDIACEAE

Rhus copallina L.
Rhus toxicodendron L.

AQUIFOLIACEAE

Ilex opaca Ait. S
Ilex verticillata (L.) Gray
Ilex glabra (L.) Gray S

CELASTRACEAE

Evonymus americanus L. S

ACERACEAE

Acer rubrum L.

BALSAMINACEAE

Impatiens biflora Walt.

VITACEAE

Psedera quinquefolia (L.) Greene

Vitis labrusca L.
Vitis rotundifolia Michx. S

MALVACEAE

Hibiscus moscheutos L. S
Hibiscus oculiroseus Britton S

HYPERICACEAE

Ascyrum hypericoides L. S
Hypericum canadense L.
Hypericum gentianoides (L.) BSP.
Hypericum virginicum L.

VIOLACEAE

Viola pedata L. S
Viola cucullata Ait.
Viola lanceolata L.
Viola primulifolia L.

LYTHRACEAE

Decodon verticillatus (L.) Ell.

MELASTOMACEAE

Rhexia virginica L.
Rhexia aristosa Britton S
Rhexia mariana L. S

ONAGRACEAE

Ludvigia alternifolia L. S
Ludvigia sphaerocarpa Ell. S
Ludvigia linearis Walt. S
Ludvigia palustris (L.) Ell.
Epilobium angustifolium L. N
Oenothera biennis L.

HALORAGIDACEAE

Proserpinaca palustris L.

UMBELLIFERAE

Eryngium aquaticum L. S
Hydrocotyle umbellata L. S
Ptilimnium capillaceum (Michx.) Raf. S
Cicuta maculata L.
Sium cicutaefolium Schrank.
Oxypolis rigidior (L.) Coult. & Rose var. *ambigua* (Nutt.) Robinson S

CORNACEAE

Cornus florida L.
Cornus amomum Mill.
Nyssa sylvatica Marsh.
Nyssa biflora Walt. S

ERICACEAE

Clethra alnifolia L.
Monotropa uniflora L.
Rhododendron viscosum (L.) Torr.
Rhododendron nudiflorum (L.) Torr. S
Kalmia latifolia L.
Kalmia angustifolia L.
Leucothoë racemosa (L.) Gray S
Lyonia ligustrina (L.) DC.
Epigaea repens L.
Gaultheria procumbens L.
Vaccinium virgatum Ait. S
Vaccinium corymbosum L.
Vaccinium atrococcum (Gray) Heller

PRIMULACEAE

Lysimachia terrestris (L.) BSP.

OLEACEAE

Fraxinus pennsylvanica Marsh. var. *lanceolata* (Borkh.) Sarg.
Chionanthus virginica L. S

GENTIANACEAE

Centaurium pulchellum (Sw.) Druce S
Gentiana saponaria L. S
Bartonia virginica (L.) BSP.
Obolaria virginica L. S

ASCLEPIADACEAE

Asclepias incarnata L. var. *pulchra* (Ehrh.) Pers.

CONVOLVULACEAE

Ipomea coccinea L. S
Cuscuta compacta Juss. S

LABIATAE

Prunella vulgaris L.
Stachys tenuifolia Willd. S
Monarda punctata L.
Lycopus virginicus L.
Lycopus rubellus Moench. S

SCROPHULARIACEAE

Linaria canadensis (L.) Dumort
Chelone glabra L.
Mimulus ringens L.
Mimulus alatus Ait.
Gratiola virginiana L. S
Gerardia purpurea L. S
Pedicularis lanceolata Michx. N

BIGNONIACEAE

Tecoma radicans (L.) Juss. S
Bignonia capreolata L. S

ACANTHACEAE

Ruellia ciliosa Pursh. var. *parviflora* (Nees) Britton S

RUBIACEAE

Galium Claytoni Michx.
Diodia virginiana L. S
Diodia teres Walt. S
Mitchella repens L.
Cephalanthus occidentalis L.
Houstonia caerulea L.

CAPRIFOLIACEAE

Lonicera japonica Thunb. S
Lonicera sempervirens L.
Viburnum dentatum L.
Viburnum cassinoides L.
Viburnum nudum L. S
Viburnum prunifolium L. S
Sambucus canadensis L.

LOBELIACEAE

Lobelia cardinalis L.
Lobelia puberula Michx. S
Lobelia inflata L.

COMPOSITAE

Vernonia noveboracensis Willd. S
Elephantopus tomentosus L. S
Elephantopus nudatus Gray S
Eupatorium purpureum L.
Eupatorium serotinum Michx. S
Eupatorium hyssopifolium L. S
Eupatorium verbenaefolium Michx. S
Eupatorium rotundifolium L. S
Eupatorium pubescens Muhl.
Mikania scandens (L.) Willd.
Heterotheca subaxillaris (Lam.) Britton & Rusby S
Chrysopsis mariana (L.) Nutt. S
Solidago fistulosa Mill. S
Solidago rugosa Mill.
Solidago tenuifolia Pursh. S
Aster surculosus Michx. S
Aster vimineus Lam.
Aster lateriflorus (L.) Britton
Aster tradescanti L.
Aster paniculatus Lam.
Aster novi-belgii L.
Aster tardiflorus L. N
Erigeron canadensis L.
Baccharis halimifolia L. S
Pluchea foetida (L.) DC. S
Pluchea camphorata (L.) DC. S
Antennaria plantaginifolia (L.) Richards
Gnaphalium helleri Britton S
Eclipta alba (L.) Hassk. S
Rudbeckia laciniata L.
Bidens discoidea (T. & G.) Britton S
Bidens comosa (Gray) Wiegand
Bidens laevis (L.) BSP. S
Bidens trichosperma (Michx.) Britton S
Helenium autumnale L.
Erechtites hieracifolia (L.) Raf.
Senecio aureus L.
Senecio tomentosus Michx. S
Krigia virginica (L.) Willd.
Lactuca canadensis L.
Hieracium venosum L.

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Further Analysis of the Pea Test for Auxin

F. W. Went

(WITH FOUR FIGURES)

INTRODUCTION AND METHODS

The pea test, although most convenient in determining the content of growth promoting substances of solutions, is little understood. So far every publication dealing with this test gave a different explanation of its mechanism (Went 1934, Jost and Reiss 1936, van Overbeek and Went 1937, Thimann and Schneider 1938).

In spite of the differences in views of the various authors, all now agree that the pea test is a differential growth phenomenon. As such it has to be studied by measuring the growth. This is not so easy, however, since it is difficult to get accurate length measurements of a strongly curved object. Van Overbeek and Went (1937) marked the pea stems with India ink before splitting; after a certain time when the major part of the growth was completed the marks, which originally were 1 mm. apart, were again measured. For the present investigation, the method was simplified by marking the stems with a suspension of lampblack in lanoline. For this purpose the stems were carefully rolled over a frame, strung with fine wires exactly 1 mm. apart and covered with a very thin layer of lanoline. Then they were split and placed in solutions of indole acetic acid. After various periods the stems (B Fig. 1) were taken out of the solution and gently pressed against a piece of paper (C), by rolling a thin glass rod (A) over them. The marks, which do not dry up, were thus transferred to the paper, and their distances apart could easily be measured. This method has many advantages. In the first place it leaves a permanent record; secondly the marks on the curved pea stem are projected in the plane of the paper, which makes measuring much easier and more accurate. After the first recording there is enough lanoline left on the stem if one or two more prints are desired. It is thus possible to measure the growth of any length of stem, without having to measure the marked intervals individually. Generally only the marks on the convex or outside (o in mm.) were transferred. By measuring the thickness of the stem (d in mm.) and the curvature (c in degrees) the length of the inside (i in mm.) was calculated: $i = o \cdot c/114 \cdot d$. Fig. 1 shows how the marks are transferred, together with an actual record.

EXPERIMENTS ON THE MECHANISM OF THE CURVATURES

A discussion of the experiments should be opened with a warning. Although the gross sensitivity of the pea may vary within certain limits

on different days, qualitatively the same curvatures are obtained. But there may be unexpected and great differences in the type of reaction. Van Overbeek and Went (1937) showed that peas, infiltrated with indole acetic

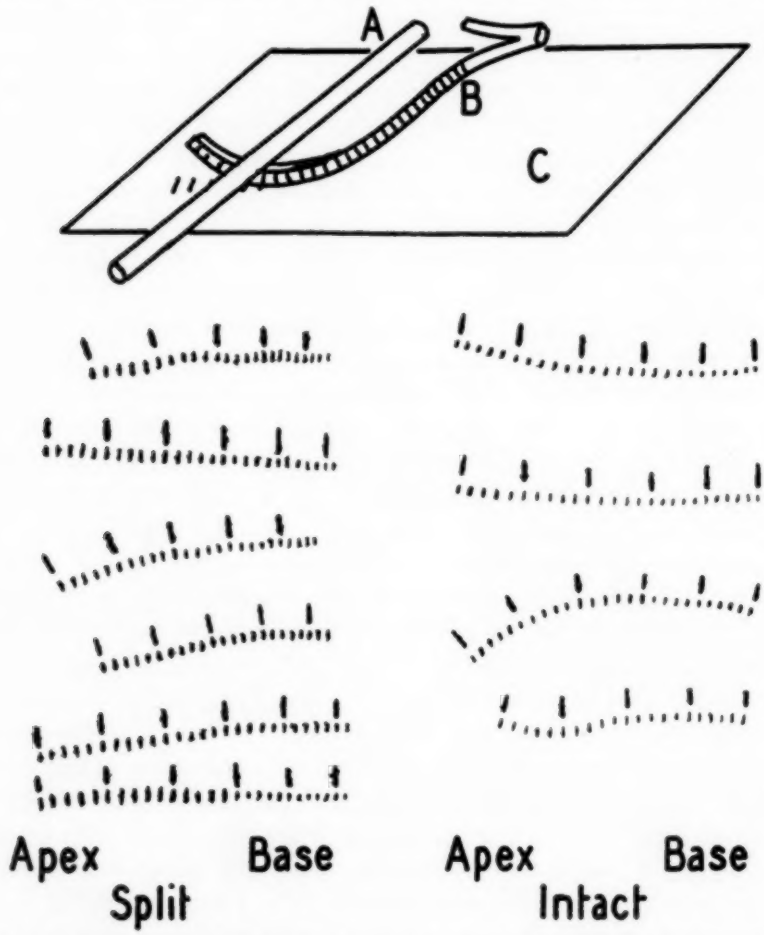

Fig. 1. *Above:* pea stem (B), which was marked with black lanoline before splitting. By gently rolling a small rod A over the stem, the marks are transferred to the paper (C). *Below:* actual record. For convenience every fifth mark is indicated by an ink mark above. The zones near the apex have grown most, in the 24 hours that they were left in indole acetic acid 4 mg./l. *On left:* marks from stems split after marking, *on right:* stems left intact.

acid immediately after splitting did not show any inward (growth) curvatures. Thimann and Schneider (1938) on the other hand claim that in two experiments the infiltrated peas showed normal inward curvatures. This experiment has been repeated innumerable times, and it was found

that in about half the cases no curvatures, in the other cases weak to good pea tests were obtained after infiltration. A general correlational analysis did not reveal the cause of these differences. Other discrepancies are the apparent activity of phenyl butyric acid on some days, and its complete inactivity on others. Also the inability of Jost and Reiss (1936) to obtain pea test curvatures, must be credited to such differences in the experimental material.

Many of the complex phenomena of the pea test have not been described yet. Still they all should be known and explainable on the basis of a valid theory. Therefore first a number of facts will be established, which will be discussed later.

Table 1 gives the summary of one experiment (several others gave the same result) in which the growth of 5 mm. zones of intact and split pea stems are compared, when placed various times after cutting and marking

TABLE 1

Etiolated pea stems cut 5 mm. below 4th node (bearing 1st leaf) and just below 3rd node, then marked and either split or left entire. Placed in indole acetic acid solutions immediately afterwards or after 4 or 9 hours washing in water. Growth in mm. of the most apical, and the next two 5 mm. zones. All figures the mean of 6–10. Plants measured 24 hours after cutting and marking.

INDOLE ACETIC ACID CONCENTRATION			4 mg./l.			0.5 mg./l.			0
Length of washing period between marking and placing in indole acetic acid			0	4 Hrs.	9 Hrs.	0	4 Hrs.	9 Hrs.	Control in H_2O
Entire stem		Top 5 mm. zone	4.7	4.5	3.1	4.2	3.0	2.0	1.2
		Second 5 mm. zone	3.2	2.6	1.8	3.0	1.9	0.9	1.1
		Third 5 mm. zone	1.7	1.5	0.8	1.8	1.1	0.6	0.8
		Total 15 mm. zone	9.6	8.6	5.7	9.0	6.0	3.5	3.1
Split stem	outside	Top 5 mm. zone	3.4	2.7	2.1	2.9	1.7	1.6	0.8
		Second 5 mm. zone	2.1	1.6	0.8	2.0	1.0	0.7	0.6
		Third 5 mm. zone	1.5	0.7	0.4	1.4	0.4	0.3	0.5
		Total 15 mm. zone	7.0	5.0	3.3	6.3	3.1	2.6	1.9
	Curvature		209°	240°	104°	122°	86°	25°	+88°
	Growth of inside								
		Total 15 mm. zone	4.6	2.3	2.1	4.9	2.1	2.3	2.4

in indole acetic acid solutions of 4 and 0.5 mg./l, and in water. Each figure is the mean of the individual measurements of 6–10 pea stems, and represents the increase in length of the zones 24 hours after marking them. A large number of conclusions can be drawn (all corroborated by other experiments).

1. When placed immediately in the solutions, the strong and the weak indole acetic acid gave approximately the same reaction as far as growth

was concerned. However, the pea test curvatures were much less in the weaker solution. But when 4 or 9 hours had elapsed before transferring the peas to auxin, the growth in the weak solution was much weaker.

2. Although the total growth was much less after 4 hours in water, the pea test curvatures in the stronger solution were considerably larger than after immediate transfer into the auxin. Together with 1 it is clear that there is no direct correlation between absolute growth of the outside and pea test curvatures.

3. The decrease in reactivity is least pronounced in the apical zones, the more basal zones have lost the power to respond to indole acetic acid after 9 hours in water. This corresponds to a very different type of curvature. When stems are placed in auxin solutions immediately after splitting, the curved zone is quite long—more than 20 mm.—and the radius of the curvature is large too. With longer intervals in water before placing them in auxin the total curvature increases or decreases, but is restricted to an increasingly shorter zone, with a decrease in the radius of curvature.

4. The reactivity to auxin of the inside is only present immediately after splitting, but after 4 hours in water and in another experiment after 2 hours already the inside fails to react at all.

TABLE 2

Alaska peas, 7 days old, cut and split in the standard manner, then infiltrated or not, and immediately or after 2 and 4 hours shaking in water transferred to an indole acetic acid solution of 4 mg./l. Curvature measured after 24 hours, means of 16–22 halves.

WHEN IN INDOLE ACETIC ACID	IMMEDIATELY	AFTER 2 HOURS	AFTER 4 HOURS
Not infiltrated	252±23	391±34	211±23
Infiltrated with H_2O	1	88	150±21
Infiltrated with indole acetic acid 0.2 mg./l	43	104	166

5. The reactivity of the outside slowly drops after cutting; the reactivity of the inside, however, drops much more rapidly, so that the pea test curvatures first increase and after that again decrease with increasing time between splitting and immersion in auxin solutions. This is also the reason why in the standard pea test the split stems are washed in water for at least 2 hours (in the present work mostly 4 hours). To show that the increased pea test curvatures after washing for some hours in water is not a single exception, table 2 presents an experiment in which the split pea stems were left in water for 0, 2 or 4 hours, before they were transferred to indole acetic acid 4 mg./l. One third of the peas was infiltrated with water, the second third was infiltrated with a solution of 0.2 mg. indole acetic

acid per liter, and the last third was left uninfiltrated. The results show that the pea test curvatures increased, when 2 hours elapsed between splitting of the peas and auxin application. After that they decreased again. In other experiments the increase in curvature was not so sudden, but continued for 4 hours at least (see table 1). In many experiments this initial rise was not found (see fig. 4). Also in the experiment of table 2, in the peas immediately placed in auxin the curved zone was long, and the radius of curvature large (6 mm.). After two hours washing the radius of curvature was much decreased (3.7 mm.), the curved zone also shortening and after 4 hours these decreases had continued (radius 3.3 mm.).

When infiltrated with either water or indole acetic acid and immediately immersed in indole acetic acid 4 mg./l., no or very small curvatures developed. That the infiltration in itself did not prevent curva-

TABLE 3

Pea test curvatures, in degrees, when peas were infiltrated either before or after splitting. The curvatures were all carried out in an indole acetic acid solution of 1 mg./l.

TYPE OF TREATMENT	CURVATURE PER STEM	NUMBER OF SPLIT STEMS
Not infiltrated, after splitting in indole acetic acid 1 mg./l.	217 ± 16	34
Infiltrated with H_2O, then split, then immediately in auxin	4 ± 3	44
Split, immediately infiltrated with indole acetic acid 1 mg./l., then in auxin	1	44
Split, after 2 hours infiltrated with indole acetic acid 1 mg./l., then in auxin	81 ± 13	34
Split, immediately infiltrated with water, then in auxin	0	44

ture is shown by those peas which were washed for 2 or 4 hours between splitting and infiltration. When placed in indole acetic acid after this period of washing good curvatures developed.

The rapid loss of reactivity is not limited to the cells along the longitudinal cut surface, but this phenomenon is also observed in the cells near the apical cut. When peas were not split, and placed in indole acetic acid 4 mg./l. immediately after cutting and marking, the two most apical 1 mm. zones elongated 0.9 and 1.0 mm. respectively. But after 4 hours washing these zones grew 0.6 and 0.9 mm. only. In the intact peas of fig. 1 this phenomenon is also very marked. The most apical 1 mm. zone has grown less than the next 5 zones. These peas were washed for $2\frac{1}{2}$ hours between cutting and placing them in the indole acetic acid 4 mg./l. solution. Thus we may conclude that the rapid loss of the ability to respond to auxin is a property of all cells close to a cut surface, whether it is a longitudinal or a cross cut. Due to the elongated form of the cells in the

pea stem we might expect the effect in the former case to be more localized than near a cross cut.

Other experiments (see e.g. table 3) indicated that it is of little importance whether the peas were infiltrated before or after splitting. Also it did not make any difference whether the infiltration took place with water or indole acetic acid, when afterwards the peas were all placed in an indole acetic acid solution. On days when the infiltrated peas gave good curvature, these were the same whether infiltrated before or after splitting. Tables 2 and 3 give additional evidence that often no auxin curvatures appear after infiltration, so that any hypothesis about the mechanism of the pea test should include this phenomenon.

If the pea test were due to a differential response of the inner and outer tissues it would be expected that the position of the split, whether near the margin or through the center, would make a great difference in the extent of the curvature. It seems hard to imagine that tearing the epidermis off one side would give any appreciable curvature at all, unless the epidermis alone were the reactive tissue. This, however, is not the case, since peeling of a halved stem which started to curve in auxin, increased the incipient curvature. Besides, the epidermis along the sides would tend to counteract the appearance of a curvature. In "pea tests" carried out with Avena coleoptiles especially it seems impossible to uphold this hypothesis since there is no inner core, and the epidermis and parenchyma cells are placed in such a way that only when the halved cylinder would roll out flat an auxin curvature would develop. And just the contrary is the case. Therefore, a crucial experiment was carried out with Avena coleoptiles. Their cylindrical form allows cutting longitudinal strips of tissue (see fig. 2), along the broad or narrow side of the coleoptile, in which the two wounded sides lie at opposite sides, symmetical in relation to the rest of the tissue, as in strips No. 1, 2, 7 and 8. The other two sides are inner and outer epidermis respectively. Such strips would be ideal for differential tissue growth curvatures, but could not give curvatures due to loss of reactivity of the cells near the wound. And indeed such strips did not show a trace of the "pea test" curvatures in indole acetic acid 2 or 4 mg./l. But whenever the wounded sides were both situated towards one side of the strip of coleoptile as in strips 3, 4, 5 and 6, fig. 2, inward curvatures resulted. In a special experiment it was determined that the narrow strips which bent outward in indole acetic acid 4 mg./l., grew a measurable amount (13% more than the water controls, measured along the outer epidermis, so that the inner epidermis must have grown still more), indicating that the outward curvature was accompanied by growth. The wide coleoptile strips

which bent inward grew somewhat more (19%) which might be expected on account of the relatively smaller effect of the wound.

In a few experiments the relation between the thickness of the split pea stem and its auxin curvature was determined. Fig. 3 combines the results of 3 experiments, and it will be seen that the curvatures of the stems from which the epidermis only has been torn off one side are almost as large as those of evenly split stems. When the growth of the zones was measured it was found that in the very wide halves the outside grew about

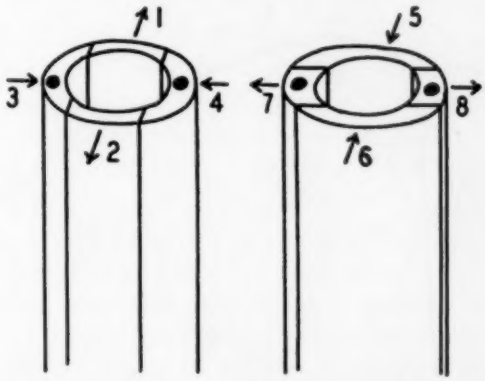

Fig. 2. Schematic picture of the way Avena coleoptiles were cut to obtain strips of tissue in which the wounded sides were symmetrically located towards the rest of the tissue (strips 1, 2, 7, and 8). The arrows indicate the sense of bending when placed in indole acetic acid 2 or 4 mg./l. The black dots represent the cross sections through the vascular bundles.

as much as an intact stem, which means that the wound was so far away from this side that it did not appreciably affect its growth. The narrower the split stem, however, the more the growth of the intact side was affected. The effect of the wound on the cut side was more nearly the same, and especially when the net effect of the indole acetic acid was calculated for thick and thin halves, the maximal differences for the inside were only 1.4 mm. against 4.3 mm. for the outside. When we consider that in the very wide and in the narrow halves the reacting inside tissues must have been cortical parenchyma, whereas in the wide and in the equal halves this was more centrally located tissue, we see that also these measurements do not support Thimann and Schneider's idea, that the central tissues would react less to auxin than the peripheral tissues. They fit in very well with the hypothesis, that the reactivity of the tissues decreases due to the wound, irrespective of where the wound is located.

Some experiments were carried out, removing the epidermis from the pea stems. Under those conditions completely different reactions were obtained. When peas were split in the ordinary way, and immediately afterwards the epidermis was removed on the side opposite the first cut surface, so that the wound effect was symmetrical on both sides of the halved stem, then distinct pea test curvatures developed; these curvatures, however,

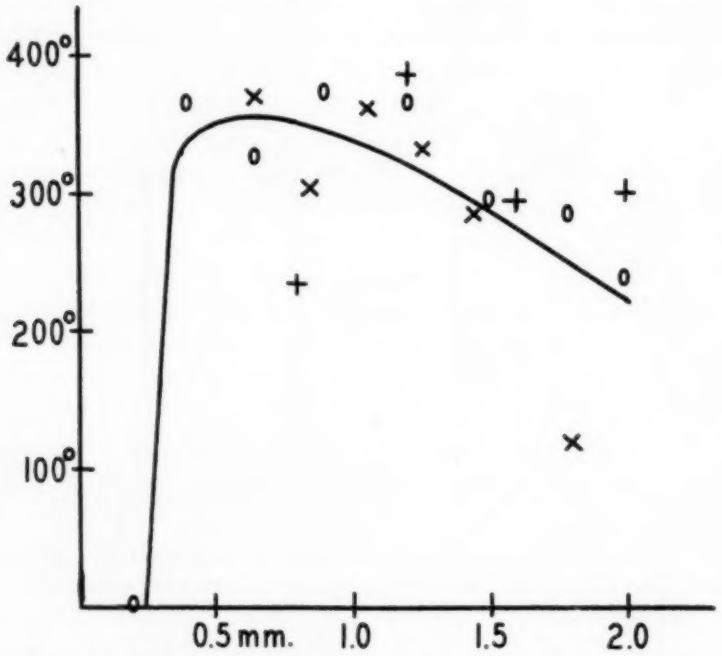

Fig. 3. Relation between thickness of the split pea stem (abscissa) and curvature (ordinate) in three different experiments, when unequally split stems have been lying in indole acetic acid 4 mg./l. for 20 hours. Each point is the mean of 10–20 observations.

appeared both in water and—somewhat larger—in indole acetic acid 4 mg./l. within 1–10 minutes after cutting. This indicates that these curvatures are primarily due to released tissue tension, and not to differential growth. If the epidermis was first peeled off, and then after 2 or 4 hours the stems were split, no pea test curvatures appeared at all (19°, 23° and 6° for 3 groups of plants of 20 halves each). Another indication that inward curvatures of the peeled halves were not due to differential sensitivity of the tissues, was found by infiltrating split stems and peeling them. Immediately the halves, which first were curved outward, bent inward, and remained so, although the halves with epidermis kept their outward curvatures, even when placed in indole acetic acid.

In the discussion the facts incorporated in the above experiments will be reconsidered. For the following experiments it is sufficient to know that there may be considerable difference in the pea test from day to day. The curvatures are due to the fact that the cells near the wound rapidly lose their sensitivity for auxin so that a few hours after cutting especially the tissues near the intact outside will respond to auxin.

EXPERIMENTS ON THE MECHANISM OF THE GROWTH REACTION

In the course of the testing of many different substances for activity in the pea test (see Koepfli, Thimann and Went 1938), it was found that in most cases a very clear distinction could be made between active and inactive substances, the latter never showing a trace of curvature. With some compounds, notably cyclohexane acetic acid and γ phenyl butyric acid, sometimes no trace of activity was found, but in other cases a few to many halved stems showed typical growth curvatures. Neither the magnitude of the curvature, nor the percentage of curved halves, however, bore any relation to the concentration used. To give an example of such an effect, the following typical experiment is quoted. The first figure in each group of 3 gives the concentration of cyclohexane acetic acid in mg./l. the second the percentage of stem halves with inward curvature, and the third curvature in degrees of halves which showed pea test curvatures. 60: 40%: 27°—30: 17%: 12°—12: 25%: 31°—6: 36%: 25°—3: 36%: 18°—1.2: 0%: 0°—0: 0%: 0°. This very clearly shows that the curvatures, although conditioned by cyclohexane acetic acid in concentrations above 2 mg./l., were limited by some other, internal factor.

It was soon found that this erratic behavior could be eliminated by washing the split stems for 4 hours in tap water before placing them in those solutions. Fig. 4, the mean of 2 experiments, illustrates the effect of washing the split pea stems for various periods. Whereas the activity of γ phenyl butyric acid completely disappears after 4–6 hours washing, the activity for low and high indole acetic acid concentrations, although falling off in the same period, still remains after 10 hours washing. In some respects this behavior resembles the effect of acid on straight growth: as long as sufficient auxin is present in the stem, any acid will activate this auxin and increase the growth, but when the auxin has disappeared, only true growth promoting substances will be able to induce further growth, and other acids are without effect (Bonner 1934, Thimann 1935).

This reasoning led to the discovery of the following phenomenon. Pea stems which had been split and washed in water for 4 hours, were for 2 hours placed either in water or in a solution of γ phenyl butyric acid of 100

mg./l. (pre-treatment). After that they were transferred to indole acetic acid solutions (after-treatment). It was found then that the pre-treatment with phenyl butyric acid had greatly increased the response to low indole acetic acid concentrations. Still, the pre-treatment by itself had not caused any visible effect. In tables 6 and 7 examples of this behavior are given.

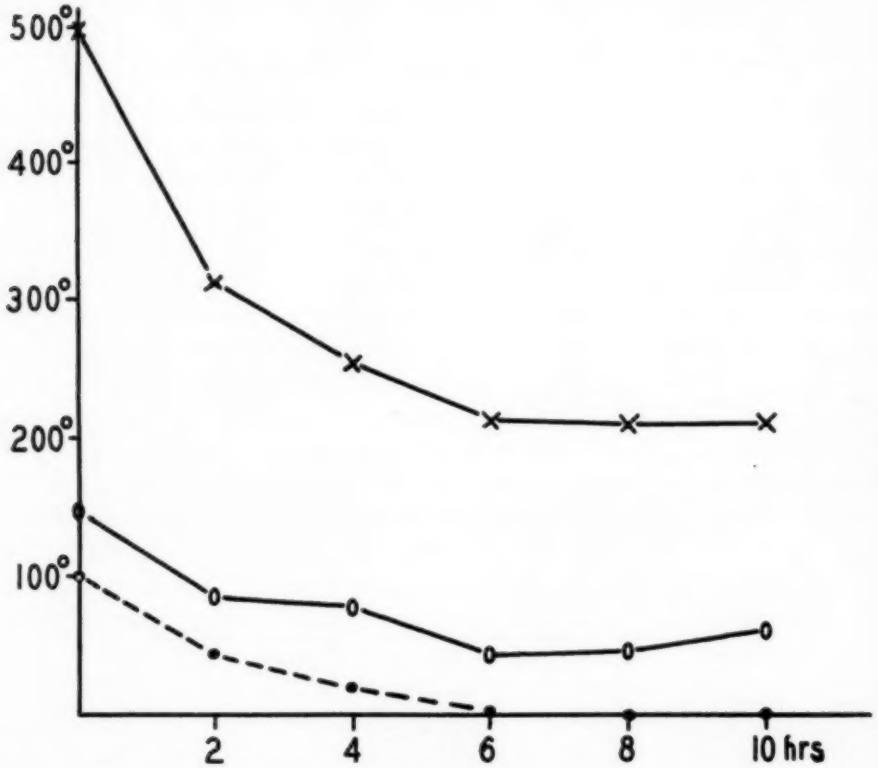

Fig. 4. Pea test curvature in degrees (ordinate), when peas are split and after various periods of washing in tap water (abscissa in hours) are placed in indole acetic acid 4 mg./l (crosses), 0.2 mg./l (circles), or γ phenyl butyric acid 100 mg./l (dots), and left in those solutions for 20 hours. Mean of two experiments. Each point represents the mean reaction of 20–40 halved stems.

It is a response which practically never fails. It also should be added that most other acids like acetic, butyric or benzoic acid do not cause a trace of such a response, so that it is not a simple acid effect.

In connection with the previous experiment the question was raised whether the effect of the phenyl butyric acid was not rather a growth inhibition, being most pronounced at the wounded side. Pea stems were marked in mm. zones and were pre-treated for 4 hours with either water or

phenyl butyric acid, and after-treated with water or indole acetic acid 0.2 mg./l. of various experiments, all giving the same results only one is reproduced in table 4. The effect of the pre-treatment is the same as if the peas had been treated with a strong indole acetic acid concentration: especially the growth of the outside is greatly increased. In another ex-

TABLE 4

Growth of etiolated pea stems, when they are split and submitted to various pre- and after-treatments.[1]

PRE-TREATMENT		AFTER-TREATMENT		GROWTH IN % OF ORIGINAL LENGTH OF	
marked, split and placed in water	in phenyl butyric acid 100 mg./l.	in water	in indole acetic acid 0.2 mg./l.	inside (wounded side)	outside (epidermal side)
				per cent	*per cent*
6 hrs.	—	10 hrs.	—	7.2	3.3
2 hrs.	4 hrs.	10 hrs.	—	7.9	7.3
6 hrs.	—	—	10 hrs.	6.8	7.9
2 hrs.	4 hrs.	—	10 hrs.	10.4	27.8

[1] Experiments of Dr. van Overbeek.

periment not reproduced in tabular form, it was found that pre-treatment did not have any effect on the non-split stems, whether they were placed afterwards in a strong or average indole acetic acid concentration. In the split stems there was no effect when after-treated with the high indole acetic acid concentration, neither as far as growth nor as curvature was

TABLE 5

Growth of 5 mm. long pea stem sections, in different pre- and after-treatments after cutting.[1]

PRE-TREATMENT		AFTER-TREATMENT		GROWTH IN % OF ORIGINAL LENGTH	
5 mm. pea stem sections in water	in phenyl butyric acid 100 mg./l.	in water	indole acetic acid 0.2 mg./l.	old peas	young peas
				per cent	*per cent*
6 hrs.	—	12 hrs.	—	9	22
2 hrs.	4 hrs.	12 hrs.	—	12	21
6 hrs.	—	—	12 hrs.	33	46
2 hrs.	4 hrs.	—	12 hrs.	33	50

[1] Experiments by Dr. van Overbeek.

concerned (cf. table 6). But with 0.5 mg./l. after-treatment the regular effect on the curvature was obtained. This was due to an increased response of the intact outside; the insides grew approximately the same. Statistically the difference is significant; for the upper 10 mm. it is 1.1 ± 0.33, or 3.5 times the standard deviation.

In another experiment (table 5) also kindly supplied by Doctor van Overbeek, also no effect of pre-treatment of intact stems with phenyl

butyric acid was observed, so that evidently this substance does not directly influence growth, and it can not be classified as a growth promoting substance or true auxin.

Another important observation which was made in all of the experiments, is that the growth response of the halved stems after phenyl butyric acid pre-treatment was more uniform than in the water pre-treated peas, so that the magnitude of the standard deviation was approximately 14% of the curvature for the pre-treated and 23% for the non pre-treated peas.

TABLE 6

Pea test curvatures in degrees after different pre- and after-treatments.[1]

PRE-TREATMENT WITH CYCLOHEXANE ACETIC ACID FOR 3 HOURS / AFTER-TREATMENT WITH INDOLE ACETIC ACID FOR 20 HOURS	100 mg./l.	50 mg./l.	20 mg./l.	10 mg./l.	5 mg./l.	2 mg./l.	H_2O
3 mg./l.	72	133	211	236			197
1 mg./l.	63	(62)	225	133	(83)	92	92
0.2 mg./l.	57	114	134	99	71		26
0.05 mg./l.	25	93	58	23		18	7
0.02 mg./l.	11	61	30	24			1
0.005 mg./l.	14	5	28	4			
H_2O	0	0	3	0	1		0

[1] Each figure is the mean of 14–18 half stems. The split pea stems were washed in water for 4 hours before pre-treatment.

The following experiments all serve to clearly establish this pre-treatment effect and its quantitative side. It is not restricted to phenyl butyric acid, but also occurs when split pea stems are treated with true auxins, and other non-auxins like cyclohexane acetic acid. The experiment of table 6 was carried out with the latter substance. It will be seen that the curvatures obtained with low auxin concentrations as after-treatment steadily increased with increasing concentrations of cyclohexane acetic acid. In all cases, however, the solution of 100 mg./l. was lower due to some toxic effect. This toxic effect is not the same every day; sometimes 100 mg./l. will be toxic, sometimes 200 mg./l. does not show any signs of toxicity. The increased sensitivity for toxic effects seems to go parallel with a decreased response to auxin (see for seasonal variations in the pea test van Overbeek and Went 1937). The maximal curvature for each after-treatment depended also on the concentration during pre-treatment: the 0.02 and 0.05 mg./l. indole acetic acid gave the largest curvatures after pre-treatment with 50 mg./l. cyclohexane acetic acid, the 0.2 and 1 mg./l. and 3 mg./l. with 10 mg./l. In summary one may

conclude that the stronger the concentration during pre-treatment the greater the effect of after-treatment with low auxin concentrations.

The effect of the pH during pre-treatment was found to be small. Thus the effect of pH on the pea test (see van Overbeek and Went 1937, D. Bonner 1938) is exerted during the after-treatment.

In further experiments based on the measurement of ca. 20,000 curved stem-halves, the quantitative relations of the "preparatory" reaction have been established. This "preparatory" reaction will be defined as that part of the chain of growth reactions, which, although without any obvious external manifestations, prepares the peas to respond, with the pea test curvatures, to very low auxin concentrations (0.1 mg./l.) which in themselves are inactive in the pea test.

The preparatory reaction requires a relatively high concentration of the active substance, even of indole acetic acid. On the other hand, the growth reaction following the preparatory reaction can be induced by exceedingly low auxin concentrations; concentrations, such as presumably exist in the normal plant. According to van Overbeek (1938) the auxin concentration in the etiolated pea stem is equivalent to 0.05 mg. indole acetic acid/l., with great variations in either direction.

We may now return to the fact mentioned before that some substances such as cyclohexane acetic acid, in most experiments cause a certain percentage of split pea stems to show growth curvatures. In those stems the auxin concentration after completion of the preparatory reaction is apparently still high enough, to act as "after-treatment." But after washing the split stems for 4 hours the auxin concentration has sufficiently dropped in most cases that no curvatures will appear any more. In one case this drop in auxin concentration was from 0.019 mg./l. indole acetic acid equivalent (see van Overbeek 1938) to 0.010 mg./l. in $5\frac{1}{2}$ hours. In experiment 80203 van Overbeek found the following decrease in auxin content: original concentration, immediately after splitting: 0.160 mg./l., after 4 hours washing 0.095 mg./l. and after 8 hours in water 0.055 mg./l. It should now be evident why the natural auxin of the pea stem is unable to induce the pea test, even though it may still cause considerable growth. The concentration of this auxin is too low to induce the preparatory reaction. Another point also may be clarified. As mentioned above auxin in very low concentrations is able to cause elongation of both inside and outside of the split stems. With such concentrations no pea test curvatures result although considerable growth may take place (van Overbeek and Went 1937). The pea test curvatures in this case are not limited by the *growth activity* of auxin, but rather the preparatory activity. Concerning the outward curvatures occurring in these low concentrations, see Discussion.

Experiments were performed to determine the effect of sugar on the component reactions of the pea test. Sucrose was used either as a pre-treatment, or was added to the auxin solutions for after-treatment. None of the sugar treatments showed any effect on the pea test curvatures obtained with low auxin concentrations. A 4% sugar solution added to the auxin caused an osmotic effect noticeable both by the decrease in rigidity

TABLE 7

PRE-TREATMENT DURING 2 HOURS WITH / AFTER-TREATMENT WITH INDOLE ACETIC ACID	H_2O	1. PHENYL ACETIC ACID				2. α PHENYL PROPIONIC ACID				3. β PHENYL PROPIONIC ACID			
		1 mg./l.	5	20	100	1 m./gl.	5	20	100	1 mg./l.	5	20	100
1 mg./l.	112	146	151	194	308	74	190	253	266	79	103	136	141
0.2 mg./l.	32	58	71	156	294	78	90	222	341	50	32	78	84
0.05 mg./l.	14	22	21	123	150	17	40	192	318	5	17	21	56
H_2O	0	0	0	16	88	0	2	32	82	0	0	0	24
CONTINUOUSLY IN PRE-TREATMENT SOLUTION	0	0	25	210	450	0	119	294	238	0	0	82	226

PRE-TREATMENT DURING 2 HOURS WITH / AFTER-TREATMENT WITH INDOLE ACETIC ACID	H_2O	4. α PHENYL BUTYRIC ACID				5. γ PHENYL BUTYRIC ACID				6. CYCLOHEXANE ACETIC ACID			
		1 mg./l.	5	20	100	1 mg./l.	5	20	100	1 mg./l.	5	20	100
1 mg./l.	112	103	76	93	124	108	122	159	232	104	163	254	199
0.02 mg./l.	32	32	35	38	33	34	47	90	102	53	67	165	156
0.05 mg./l.	14	12	5	10	8	7	26	35	142	12	29	88	116
H_2O	0	0	0	0	0	0	0	3	0	0	0	0	0
CONTINUOUSLY IN PRE-TREATMENT SOLUTION	0	0	0	0	0	0	0	0	0	0	0	0	0

of the stems in those solutions, and by the smaller curvature. In the high auxin concentrations a clear sugar effect was evident: at 2 or 3% sucrose (whether as pre- or after-treatment) the pea test curvatures were distinctly increased, suggesting that at the highest growth rates sugar became limiting, but that the preparatory reaction has nothing to do with sugar.

In this section two successive reactions, which result in the pea test curvatures have been analysed by making use of the fact that some substances may influence one and not the other of the two reactions. That both properties may be possessed by the same substance is shown in an independent way by the next experiment (table 7). Phenyl acetic, α phenyl

propionic and β phenyl propionic acids all cause good pea curvatures. If, however, the stems were taken out after 2 hours and placed in water, little or no curvatures resulted. If these pre-treated stems were placed in dilute auxin solutions the subsequent curvatures made it clear that the preparatory reaction had already taken place. In this way it was shown that the preparatory and the growth reactions differ not only in type but that with some substances they are even separated in time. This also demonstrates that the two reactions are links of a chain of reactions leading towards the pea test, and that the preparatory reaction precedes the growth reaction. The inactivity of γ phenyl butyric acid shows that a certain specificity exists for the preparatory reaction.

DISCUSSION

Now we must try to piece together the facts established in the experimental part. For the discussion it will be simplest to take the hypothesis of Thimann and Schneider (1938) as a starting point. They have disproven the hypothesis brought forward by van Overbeek and Went, that the pea test would be due to a differential auxin entry at the two sides of the split pea stem. The author is completely satisfied on this point. However, the facts presented in this paper do not agree with Thimann and Schneider's hypothesis, that the pea test is due to an innate differential reactivity of the inner and outer tissues for auxin.

To begin with all tissues in the intact pea stem seem to have the same reactivity to auxin. This is the same as Jost and Reiss (1936) have shown for Taraxacum. Perhaps the inner tissues respond slightly better than the outer tissues, but probably this is not the case. The tissue tension brought forward by Thimann and Schneider as evidence is connected with a differential elasticity of the cell walls of inner and outer tissues; the outward curvatures appear immediately and since they are completed within a few minutes they are not due to differential growth after splitting. Upon placing them in plasmolysing solution these curvatures disappear again, demonstrating that they are due to turgor, and not to growth. In the split stems the growth which still occurs in water after the initial tissue tension curvature is completed does not change the extent of this curvature, therefore, the different tissues all grow at the same rate. In fact, the curvature is so constant that de Vries (1884) could base a determination of the isotonic coefficients of solutions on the change in curvature of split stems. Whether this tissue tension is due to differential sensitivity of the tissues of the intact stem for auxin is immaterial for an explanation of the pea test, and besides it can not possibly be decided. For to determine the response of the different tissues they would have to be cut and the wounds would interfere with the normal growth rate. Besides, in the intact plant,

the inner tissues contain at least twice as much auxin as the outer layers. In one experiment the pea stems were divided into 3 strips by 2 longitudinal cuts. After extraction the inner strips, containing inner and outer tissues both gave per gram wet weight 31.°6 curvature in the Avena test, whereas the outer strips gave 15.°2 only. Another experiment gave a similar difference (28.1 against 14.8 for the outside). This is not surprising, since presumably the auxin is transported through the central cylinder, so that the inner tissues nearest the vascular elements would contain more auxin than the cortex. This fact in itself would be sufficient to account for differential growth and for the tissue tension, so that for the tissue tension curvatures of the pea stem differential response to auxin is merely an unproven hypothesis.

There is another serious objection to such a differential response of the tissues in the intact stem. When peas were infiltrated with different auxin concentrations (0.2, 1 and 4 mg./l. indole acetic acid) and allowed to grow in these solutions for 2, 4 or 8 hours, then they did not show any tissue tensions, inward or outward. This fact is also mentioned by Thimann and Schneider, but remarkably enough they consider it as an indication for differential response. But the only obvious conclusion is that the inner and outer tissues had grown at the same rate in the different auxin concentrations. Even in the 0.2 mg./l. solution, which gives only weak pea test curvatures (fig. 4, tables 6, 7), the tissue tension was released. This is a clear indication that when all cells are evenly supplied with a growth substance (the tissues were infiltrated) no differential growth takes place, and therefore, it is more likely that the tissue tension is due to differential auxin content of the inner and outer tissues.

After splitting the stem the ability of the inside to respond to indole acetic acid falls off very rapidly. After 2–4 hours its reactivity has dropped to zero. The more rapidly the auxin enters, the smaller this loss of reactivity will be; this then explains the effect of infiltration with auxin immediately before or after splitting of the peas. If the auxin acts before the drop in activity has occurred, no pea test curvatures result. An excellent confirmation of this conclusion can be found in van Overbeek and Went (1938), table 6. It will be seen that the outside of infiltrated stems has grown almost as much as in non-infiltrated stems. But the difference lies in the growth of the inside, which grows even more than the outside and much more than in any concentration in non-infiltrated stems. The criticism of Thimann and Schneider against this experiment does not hold, since in unbuffered solutions the concentration used always gave regular pea test curvatures. Besides, in the same experiment a ten times higher concentration was also used (unpublished), which caused a growth of the inside

of 7.8 mm. against 7.4 mm. in the lower concentration and 7.1 mm. of the outside. The experiment of table 2 also shows, that even when peas infiltrated with auxin immediately before or after splitting do not give pea test curvatures, they will do so when infiltrated 2 hours after the splitting, when the reactivity of the inside has decreased. In Taraxacum this loss of sensitivity of the cells bordering the wound seems to occur only when the auxin content is lowered by cutting the stems a day before the experiment (Jost and Reiss 1936).

Other peculiarities of the pea test become explainable on the basis of these facts. From the beginning, immediately after splitting the peas, there are two opposing tendencies. The first one is the loss of sensitivity of the inside tissues near the wound. This will tend to increase the curvature with increasing time between splitting and placing in auxin. But the second tendency is the loss of reactivity to auxin of the more basal zones, both of inside and outside tissues. This will restrict the curvature to a shorter zone. Now it depends which tendency is stronger whether the auxin curvature of the pea test will increase or decrease the first 4 hours after splitting, while the stems are being washed in water. Fig. 4 gives an example of an initial decrease, tables 1 and 2 of an increase in curvature within the first 4 hours.

Thimann and Schneider (1938) have laid much stress on the use of the stem-reference method for measuring the pea test curvatures, against the inflection-reference method used by the writer. In a few cases the former is indicated, e.g., when the effect of pH is under investigation (van Overbeek and Went, 1937, p. 37, D. Bonner 1938). But in most cases it complicates the interpretation of the results, since two distinct and different phenomena are being confused. One is the tendency for outward curvature, which is not restricted to the growing zone, but which is equally pronounced along the whole split section. From Thimann and Schneider's fig. 6, it even will be evident that the most pronounced outward curvature in 0.02 mg./l. indole acetic acid occurs well below the zone which will give the pea test curvature, so that the stem reference method records opposing reactions performed in different regions of the stem. Not only because this outward curvature occurs in slowly or not growing zones, it may be questioned whether it is a growth reaction at all. But also the bulk of it occurs within the first 20 minutes. So far the shortest time for the first indication of growth after auxin application has been 17 minutes (Schneider and Went 1938), but under most conditions this period is longer, and most rapid growth starts somewhat later.

Finally, this outward curvature does not or hardly occur when the split pea stems are placed in weak auxin solutions after an initial 4–6 hours

washing period in water (outward curvatures of water controls 96°, when placed immediately in phenyl acetic acid 1 mg./l. 127°, but after 4 hours washing 102°). The same phenomenon can be found in Thimann and Schneider's fig. 9, which is a most eloquent demonstration that the outward and inward curvatures are unrelated. For the inward curvatures may or may not be accompanied by an outward curvature. As a possible explanation of the outward curvatures a permeability phenomenon might be suggested, in which connection an investigation of Bouillenne (1929) might be mentioned, who worked with strips of onion leaves, which are in many respects comparable with the split pea stems. He found that certain substances in low concentrations permeated with such rapidity into the cells near the inner epidermis, that a very rapid outward curvature resulted, very much like the acid curvatures and benzofurane outward curvatures of pea stems.

In this paper the reason for the loss of reactivity of cells near the wound has not been further considered. The phenomenon itself was known, or at least postulated to explain e.g. the geotropic response of halved stems (see Went and Thimann 1937, pp. 158, 179). However, in the earlier work it was thought that the wound effect was due to auxin destruction by the wound, whereas in the present paper it was conclusively shown to be a decrease in the reactivity of the cells to auxin. It should be mentioned, that Thimann and Schneider (1938) also assume a decreased reactivity of tissue due to the influence of the wound ("damage effect") but they consider this more as a diffuse effect than one localized near the wound.

Thus in the first part of this paper it has been attempted to analyze the topographic growth relationships in the pea stem, which lead to the pea test curvatures. In the second part, the growth reaction itself has been analyzed, and has been shown to consist of two parts, which can be separated and individually measured.

There are 4 independent means of demonstrating that we have to do with 2 successive reactions, brought about by the growth promoting substances. The first one makes use of the fact, that some substances will only cause the first of the two reactions to occur, but are unable to induce the second or growth reaction proper. Such substances, which exhibit part of the properties of the auxin except the growth property, can be brought together under the name of *hemi-auxins*. It is not the purpose of this paper to discuss these hemi-auxins in detail; they only have been used as a tool. The most outstanding ones are γ phenyl butyric acid and cyclohexane acetic acid.

The second demonstration that two successive reactions, both caused by auxin, are involved in the pea test, lies in the fact that a substance like

phenyl acetic acid, before causing actual growth, will cause the preparatory reaction to occur. Thus, the two reactions can be separated in time. In indole compounds this time separation is hardly demonstrable since one seems to follow the other almost immediately.

The third difference between the two reactions is their pH sensitivity. The preparatory reaction is independent of pH, the growth reaction only occurs when sufficient undissociated acid is present inside the plant, as at low pH.

A fourth difference lies in the relative concentrations of auxin required for the two reactions. The preparatory reaction becomes negligible under 0.2 mg. indole acetic acid/l., whereas the growth reaction can be induced with less than one tenth of that concentration (table 6).

It is not possible as yet to give a satisfactory explanation of the effect of the hemi-auxins on the pea stems. It was shown that they do not affect growth by themselves. They increase the sensitivity of the cells for auxin. There are some indications that they do this by preserving or accumulating the other growth factors, of the caline or food factor type. But in another paper this will be discussed in greater detail.

As a result of this investigation the pea test can now be used for the determination of from 10 to 50 times smaller auxin concentrations than was possible before. If split pea stems are pre-treated with e.g. cyclohexane acetic acid, 50 mg./l. for 2 hours, they then will produce a curvature of 61° with 0.02 mg. indole acetic acid per liter, whereas peas not pre-treated give only 26° for 0.2 mg. auxin/l. (see table 6). The lowest indole acetic acid concentrations which can conveniently be measured with the Avena test are of the same order of magnitude (0.01 mg./l.), so that the pea test is now as suitable for the determination of low auxin concentrations as the Avena test. It has, however, one disadvantage, and that is the relatively large volume of solution required (20 cc.). The use of smaller test objects might well decrease this amount. Nevertheless for the determination of small quantities of auxin, such as occur in plant tissues, the Avena test remains indispensable. The pre-treatment has the additional advantage of making the response more uniform.

SUMMARY

The pea test curvatures, which appear when etiolated pea stems are split in their growing region and placed in auxin solutions, are due to differential growth of the tissues under the intact epidermis and the tissues bordering the wound. This is not an innate differential sensitivity of these tissues to auxin, but is due to the rapid loss of sensitivity of the tissues near the wound. If auxin reaches the cells before the loss of sensitivity

occurred, e.g., by infiltration of the split stems with an auxin solution, or by splitting them after a few hours immersion in auxin, small or no pea test curvatures result.

The effect of auxin in the pea test has been resolved into a chain of two reactions. The first is the so-called preparatory reaction, which is independent of the pH, and which can be induced by substances lacking growth activity (hemi-auxins). Indole compounds induce the preparatory reaction in relatively high concentrations (1 mg./l.). The growth reaction proper follows the preparatory reaction in time, and requires a much lower auxin concentration (appr. 0.01 mg./l. indole acetic acid).

With the aid of these new data a number of peculiarities of the pea test can be explained. A greatly improved pea test for very low auxin concentrations is described.

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A New Variety of Isoetes virginica

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(WITH ONE FIGURE)

The species *Isoetes virginica*[1] was described in 1937 from limited material collected the previous year in Augusta County, Virginia, by Lloyd G. Carr and Edgar T. Wherry. It is a matter of interest that before other stations for the species were reported, a number of stands of an *Isoetes* now considered to be a variety of *I. virginica* were found in the Piedmont in Georgia by Joseph H. Pyron and Rogers McVaugh.

Isoetes virginica Pfeiffer var. **piedmontana,** var. nov. Folia numero 15–50, longitudine 7–15 (20) cm., gracilia, basi fuscescentia, septis crassis instructa, fibrosis peripheric numero quattuor, sex vel nonnumquam nullis instructa; sporangia oblongata, brunneo-fusca, velo angusto; macrosporae diametro 400–480 μ, variatim asperis eminulis vel brevibus cristis interdum aliquantulo ramosis ornatae; microsporae longitudine 27–33 μ, spinulosae.

Leaves 15 to 50 in number, chiefly 7 to 15 (20) cm. long, slender, brown at the base; leaf septa coarse; peripheral strands four or six in number, or entirely lacking; sporangia oblong, brown, with narrow velum; megaspores 400–480 μ in diameter, marked irregularly with low rough processes and short discontinuous ridges, sometimes branching; microspores 27–33 μ in length, spinulose.

Specimens examined:

Georgia: shallow soil about granite outcrops, Echols Mill 12 miles n.e. of Lexington, Oglethorpe Co., May 13, 1938, Pyron & McVaugh 2869 (Herb. U. Geo., Mo. Bot. Gard. Herb.). TYPE: same station, Feb. 15, 1938, Pyron & McVaugh 2062, and April 4, 1938, Pyron & McVaugh 2422; moist shallow soil on flat granite rock "Heggie Rock" (emersed), 8 mi. east of Appling, Columbia Co., Pyron & McVaugh 1676; shallow soil, depressions on flat granite rocks, 4 mi. s.w. of Franklin, Heard Co., April 30, 1938, Pyron & McVaugh 2835 and 2840.

Other collections which although of immature plants are probably this same variety were made in Greene Co. (P. & McV. 1645), Putnam Co. (P. & McV. 2406), Warren Co. (P. & McV. 2050), Pike Co. (P. & McV. 2293). It is apparently of fairly wide distribution in the Piedmont, with stations, of which McVaugh says "The maximum elevation is less than 1500 ft. and some of the stations are almost within the boundaries of the Coastal Plain."

The variety can be distinguished from the species chiefly on the shorter leaf length, larger leaf number, coarser septa in the leaves, and a tendency toward more open and lower markings on the megaspores. The vegetative

[1] Pfeiffer, Norma E. A new *Isoetes* from Virginia. Claytonia **3**: 29–30. 1937.

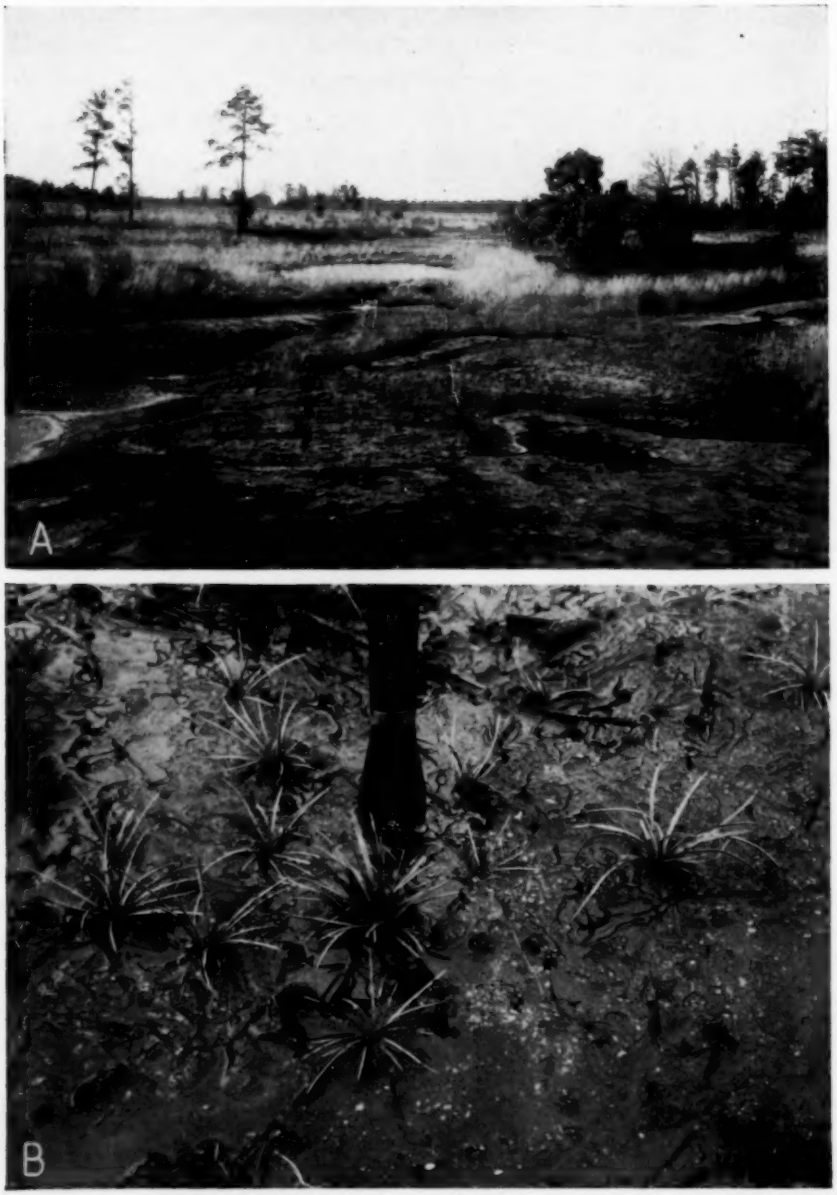

Fig. 1. A. Habitat of *Isoetes virginica* var. *piedmontana*, Greensboro, Greene Co., Ga. *Isoetes* grows in and around the pool of water which shows in the exact center of the picture. B. Detail of the plant, about $\frac{1}{3}$ natural size; photograph taken at the station 4 miles southwest of Franklin, Heard Co., Ga.

characters may be associated with the peculiar habitat, the shallow soil around the margins of flat outcrops of granite which is in distinct contrast to the "mud in a thicket bordering a meadow under water as a temporary pond in spring" in which Carr originally found the species, and the "small drainage ditch in open woodland" in Prince Edward Co., Virginia. Specimens from the latter location collected by A. B. Massey and Edith Stevens, May 13, 1938, were found on examination to resemble the previous Virginia collection and so are placed with the species.

The habitat and habit of the new variety are shown in Figure 1; the photographs were taken by Rogers McVaugh of the Division of Plant Exploration and Introduction of the Bureau of Plant Industry, who kindly obtained permission for their publication.

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Eight Undescribed Species of Melastomataceae

H. A. Gleason

Except as noted for the first species, the type specimens have been deposited in the Britton Herbarium at the New York Botanical Garden.

Tibouchina cornuta Gleason, sp. nov. Sect. *Diotanthera*: "Frutex scandens." Caules graciles, obscure 4-angulati, sparse strigosi praesertim ad angulos, pilis subulatis non glandulosis 0.4–0.7 mm. longis, ad nodos densiore setosi, pilis paulo longioribus; internodia usque 10 cm. longa superiora multo abbreviata. Petioli graciles 5–10 mm. longi, dense strigosi, pilis validis, imbricatis, 0.5–0.8 mm. longis. Laminae membranaceae, virides, subtus pallidiores, ovato-lanceolatae, usque 110 mm. longae 37 mm. latae, superiores multo minores, in quoque jugo plusminus inaequales, majoribus minores fere duplo excedentibus, acuminatae, minutissime serrulatae, ad basin cuneatae, 5-nerviae, nervis ad basin distinctis, supra strigosae, subtus ad venas substrigosae ad paginam minute pilosae. Inflorescentia pluriflora pseudo-umbelliformis, pedicellis 2–5 mm. longis. Hypanthium anguste campanulatum, 4.7 mm. longum, obscure 8–10 costatum, sparse strigosum, pilis gracilibus 0.5 mm. longis. Calycis tubus 0.5 mm. longus; sepala ligulata ultra basin late triangularem, 4.7 mm. longa, minute ciliata, parce strigosa. Petala alba, ut videtur circa 9 mm. longa. Filamenta gracilia, 5.4 vel 6.9 mm. longa; thecae anguste subulatae, leviter curvatae, 3.9 vel 5.2 mm. longae; connectiva curvata, infra thecas 0.8 vel 1.3 mm. producta ad summum filamenti, infra filamentum lobis 2 obtusis oblongis 0.8 mm. longis (in minoribus) vel 2 subulatis divergentibus recurvis 2 mm. longis (in majoribus) ornata. Ovarium summo setis circa 15 erectis subulatis coronatum; stylus leviter sigmoideus, 8.4 mm. longus.

Type, *Mexia 4296*, collected in virgin forest at Colaya, Prov. Sur Yungas, Dept. La Paz, Bolivia, alt. 1870 meters, and deposited in the Gray Herbarium. The species is intimately related to *T. capitata* Cogn. and *T. membranifolia* Cogn., also from Bolivia, and is most readily distinguished by its long sepals, those of its two relatives being triangular and scarcely 2 mm. long.

Conostegia hispida Gleason, sp. nov. Frutex 3 m. altus. Rami validi, obscure quadrangulati, dense hispidi, pilis subulatis, 2.5 mm. longis. Petioli validi, 25 mm. longi, densissime hirsuti. Laminae membranaceae, ellipticae, usque ad 22.5 cm. longae 12.5 cm. latae, abrupte acuminatae, grosse repando-dentatae, ad basin cuneatae, 5-nerviae, jugo exteriore submarginali, jugo intermedio ad basin venae mediae approximato, supra juventute sparse hirsutae mox glabrae, subtus ad paginam sparse ad venas dense setosae; nervi secundarii 8 mm. dissiti ad angulum 75° orientes. Inflorescentia terminalis, sessilis, pluriflora, dense congesta, ubique hirsuta; flores breviter pedicellati, (5 vel)

6-meri. Alabastra ellipsoidea, hirsuta, 11–12 mm. longa, rostro lineari tereti 3 mm. longo ornata. Hypanthium poculiforme, 5 mm. longum, dense hirsutum, pilis flexuosis vel crispatis, 2 mm. longis. Petala alba, triangulari-obovata, 12–13 mm. longa, 10–11 mm. lata, oblique truncata, plusminus erosa. Stamina 30 isomorpha; filamenta gracilia, 4.2–4.7 mm. longa; antherae complanatae, 2.9–3.2 mm. longae, 4-loculares, poro ventro-terminali dehiscentes, thecis infra apicem filamenti productis; connectivum elevatum exappendiculatum, supra apicem filamenti gibbosum. Ovarium inferum, 6-loculare, summo truncato-conico glabro. Stylus 7–8 mm. longus, superne leviter dilatatus; stigma capitatum.

Type, *Mexia 8430*, collected at Parroquia de Concepcion, Prov. Esmeraldas, Ecuador, alt. 105 meters. In leaf characters and pubescence *C. hispida* is similar to *C. setosa* Triana, of Colombia. It differs in leaves glabrous above and lacking bullae at the base, in its much larger flowers, in its greatly congested panicle, and in the presence of thirty stamens.

Conostegia multiflora Gleason, sp. nov. Arbor 24 m. alta. Rami 4-angulati, 4-sulcati, minute sparseque furfuracei. Petioli graciles, 15–20 mm. longi, minute stellato-furfuracei. Laminae firmulae, ellipticae vel elliptico-obovatae, usque ad 16 cm. longae 8 cm. latae, breviter abrupteque acuminatae, apice ipso obtuso, integrae vel obscure repandae, dentibus rotundatis, basi late acutae, 5-nerviae, jugo exteriore submarginali, supra virides, minutissime albo-punctatae, glabrae vel ad venas primarias minutissime furfuraceae, subtus pallidiores, ad venas minute stellato-furfuraceae ceterum glabrae; nervi primarii supra leviter impressi, subtus prominentes, secundarii utrinque plani sub angulo circa 75° adscendentes, tertiarii subtus reticulati. Inflorescentia paniculata, ramosa, multiflora, 15 cm. longa, axibus angulatis et ramis divaricatis minute stellato-furfuraceis; bracteae deciduae; pedicelli 1 mm. longi. Flores 5-meri. Hypanthium suburceolatum, 2.5 mm. longum, glabrum, in sicco ut videtur scabrellum. Calyx in alabastro ovoideus, glaber, rotundatus, 2.5 mm. longus. Petala oblonga, 4 mm. longa, 1.8 mm. lata, apice rotundata, saepe latere uno lobata. Stamina 10 isomorpha; filamenta gracilia, 2.1 mm. longa; antherae oblongae, non compressae, 4-loculares, 2 mm. longae, thecis infra insertionem filamenti in lobos 2 rotundatos breviter productis, connectivo simplici. Ovarium inferum, 7-loculare, summo subplano; stylus crassus 2.3 mm. longus, stigmate subgloboso, 0.8 mm. alto.

Type, *Mexia 8409*, collected at Parroquia de Concepcion, Prov. Esmeraldas, Ecuador, alt. 105 meters. The species is related to *C. Poeppigii* Cogn., which has acute buds, 6–8-merous flowers, and a truncate stigma.

Miconia cayumbensis Gleason, sp. nov. Sect. *Glossocentrum:* Arbor 10 m. alta. Rami teretes graciles, juventute dense sed tenuiter stellato-canescentes, demum furfuracei; internodia 3–5 cm. longa. Petioli crassiusculi, 5–8 mm. longi,

stellato-canescentes. Laminae firmulae, ellipticae vel oblongae, usque ad 16 cm. longae 6 cm. latae, breviter acuminatae, obscure remoteque denticulatae, basi acutae, 3-nerviae, jugo inconspicuo marginali neglecto, supra glabrae, subtus minutissime stellatae, pilis 0.05 mm. diam.; venae supra planae, subtus prominulae; secundariae 4–5 mm. dissitae, sub angulo fere recto divergentes; tertiariae subtus reticulatae. Inflorescentia paniculata ramosa, fere 10 cm. longa, ut rami pubescens. Flores sessiles, 5-meri. Hypanthium campanulatum, 1.7 mm. longum, obscure 10-costatum, tenuissime stellato-canescens. Calycis stellato-canescentis tubus 0.3–0.4 mm. longus; sepala late semicircularia 0.3–0.4 mm. longa, dentibus exterioribus minutis callosis. Petala anguste obovato-oblonga, 2.8 mm. longa 1.6 mm. lata, superne rotundata. Stamina dimorpha. Filamenta gracilia 3.3 vel 2.8 mm. longa. Antherae crasse lineares, thecis 2.6–2.7 vel 2.3–2.4 mm. longis, in ser. ext. poro ventro-terminali dehiscentes, in ser. int. poro terminali. Connectivum ser. ext. basi 0.6–0.7 mm. productum in lobum unum dorsalem curvatum, apicem filamenti semiamplectentem; ser. int. 0.4–0.5 mm. longum in lobum 1 dorsalem et 2 laterales divisum. Ovarium semi-inferum, 2-loculare, summo truncato-conicum glabrum. Stylus glaber, declinatus, fere 7 mm. longus; stigma capitatum.

Type, *Mexia 8285*, collected near the mouth of the Río Cayumba, Dept. Huanuco, Peru, alt. 880 meters. The width of the anther pore definitely suggests that *M. cayumbensis* belongs in the section Eumiconia. Nevertheless, when a more natural classification of this huge genus is developed, it will probably be placed near *M. longifolia* and *M. minutiflora*, now assigned to the section Glossocentrum. Most Andean species of this section have isomorphic stamens; of those with dimorphic stamens *M. longifolia* is distinguished from our species by its pli-veined leaves, and *M. minutiflora* and *M. puberula* by leaves rounded at the base.

Miconia cremadena Gleason, sp. nov. Sect. *Cremanium:* Frutex 5 m. altus; rami 4-sulcati dense subtomentosi, pilis crassis brunneis ad 1 mm. longis, internodiis usque 5 cm. longis. Petioli validi, 3–4 cm. longi, quam caules densius pubescentes. Laminae tenues, laete virides, anguste ellipticae, usque 29 cm. longae 9 cm. latae, longe acuminatae, integrae, basi acutae, 3-nerviae jugo marginali neglecto, supra glabrae, subtus ad venas primarias sicut petioli dense pubescentes, ad superficiam et venas minores villosae, pilis usque 2 mm. longis; venae secundariae sub angulo circa 80° orientes 5 mm. dissitae. Panicula ampla, ramosa, 20 cm. longa lataque, pubescens; pedicelli 1 mm. longi. Flores 5-meri. Hypanthium poculiforme, ad torum 3.2 mm. longum, carnosum primum sparse furfuraceum deinde verisimiliter glabrum, sub lente minutissime glandulosum, glandulis stipitatis 0.04 mm. longis. Calycis tubus fere erectus, 0.4 mm. longus, sinibus late acutis; sepala triangulari-ovata, a toro 1.4 mm. longa, margine scariosa; dentes exteriores late triangulares adpressi, sepala aequantes. Petala orbicularia, alba, glabra, avenia, equilatera, vix retusa, 3 mm. longa lataque. Stamina isomorpha; filamenta 3.9 mm. longa,

supra medium geniculata, glanduloso-pubescentia praesertim apicem versus; antherae obovoideae, 2.1 mm. longae, 4-loculares sed 2-porosae, septis apicem non attingentibus, thecis 1.4 mm. longis; connectivum infra thecas valde dilatatum in carinam dorsalem et ventraliter obscure 2-lobatum, saepissime pauciglandulosum. Ovarium inferum, 2-loculare, summo glabrum; stylus rectus, 6.5 mm. longus, hinc inde glandulosus, stigmate truncato 1.1 mm. diametro.

Type, *Skutch 3394*, collected in woods and thickets at Vera Blanca de Sarapiquí, Costa Rica, between Poás and Barba Volcanoes, alt. 2050 meters. In its glandular filaments it differs from all other species of *Cremanium* known to me. Its anthers are equally distinctive.

Clidemia ecuadorensis Gleason, sp. nov. Sect. *Staphidium:* Frutex glaber 3.5 m. altus. Rami obscure 4-angulati. Petioli graciles, 5–10 mm. longi. Laminae membranaceae, ellipticae, usque ad 17 cm. longae 5.5 cm. latae, apice longe caudatae, cauda lineari 25–35 mm. longa, integrae, basi acutae, 5-pli-nerviae; vena media utrinque elevata, cum venis lateralibus interioribus basi saccato-connecta; venae tertiariae insigniter reticulatae. Inflorescentiae axillares, e basi polychotomae, ramis valde divaricatis. Flores subsessiles, 5-meri, jam immaturae. Hypanthium poculiforme, ca. 2.5 mm. longum. Calycis dentes exteriores subulati, 1 mm. longi, sepala triangulari-ovata brevia multo excedentes. Petala alba decidua, immatura triangulari-ovata obtusa enervia. Antherae oblongae, connectivo non appendiculato. Ovarium inferum 3-loculare. Stylus maturus 5 mm. longus, superne conspicue dilatatus, stigmate ut videtur truncato. Fructus atropurpureus baccatus.

Type, *Mexia 8431*, collected at Parroquia de Concepcion, Prov. Esmeraldas, Ecuador, alt. 105 meters. In spite of the immature condition of the flowers, there seems little room for doubt that the species is properly assigned to *Clidemia*, within which it can not be referred to any described species. In all features of habit it is strongly suggestive of *C. japurensis* and *C. naevula*, glandular-pubescent species of Amazonia. *C. ecuadorensis* is also well characterized by the caudate appendages of the leaves.

Clidemia gracilipes Gleason, sp. nov. Sect. *Sagraea:* Frutex ramosus fere metralis. Caules superiores graciles, purpurascentes, fere glabri. Petioli graciles, divaricati, 1–4.5 cm. longi, inferne fere glabri, superne pubescentes, pilis incurvis 0.1 mm. longis. Laminae membranaceae atrovirides, in quoque jugo saepe inaequales, ovatae, majores 12 cm. longae 6 cm. latae, minores 4 cm. longae, 2 cm. latae, superiores vix reductae, acuminatae, vix serrulatae et minute ciliatae, basi late rotundatae vel cordulatae, 5-nerviae, supra fere glabrae, albo-punctatae, subtus ad primarias sicut petioli pubescentes, ad superficiem glabrae. Paniculae laxae, ramosae, ad 10 cm. longae, axibus minute sparseque hirtellis, ramis gracillimis elongatis divaricatis glabris; pedicelli ut videtur elongati, pedicellis veris 1 mm. longis bracteis 2 subulatis vix 1 mm.

longis sustentis. Flores 4-meri. Hypanthium campanulatum, purpureum, ad torum 2.6 mm. longum, minutissime pubescens, pilis incurvis 0.04 mm. longis. Calycis tubus patulus, 0.3 mm. longus; sepala late triangularia e sinibus rotundatis, 0.7 mm. longa, acuta; dentes exteriores crasse subulati, divaricati, 1 mm. longi. Petala alba, oblongo-ovata, 2.6 mm. longa, obtusa, latere tecto obscure crenato. Stamina 8 isomorpha; filamenta crassa, glabra, 1.4 mm. longa antherae oblongae, obtusae, 2-loculares, 1.6 mm. longae, connectivo simplici. Ovarium inferum, 3-loculare, summo plano glabro. Stylus gracilis, glaber, 4.8 mm. longus, stigmate truncato.

Type, *Mexia 9262*, collected in partial shade at Santa Maria, District Choapam, Oaxaca, altitude 1500 m. *Clidemia gracilipes* is closely related to *C. cymifera* Donn. Sm. of Guatemala, agreeing with it in general habit, style, stamens, and calyx. *C. cymifera* differs from ours in having much larger petals, a four-celled ovary which is only two-thirds inferior, much shorter panicles, thicker leaves, and stellate pubescence.

Blakea Mexiae Gleason, sp. nov. Sect. *Eublakea:* Arbor 12 m. alta. Rami teretes, juveniles arcte ferrugineo-tomentosi, pilis barbatis 0.5–1 mm. longis, pilis simplicibus 1–2 mm. longis intermixtis, vetustiores glabrescentes. Petioli 10–15 mm. longi ferrugineo-tomentosi. Laminae subcoriaceae pallide virides ellipticae, usque ad 12 cm. longae 6 cm. latae, acuminatae, integrae, basi cuneatae vel acutae, 3-nerviae, jugo marginali praetermisso, supra juventute ferrugineo-tomentosae mox glabrescentes vel ad venas prope basin persistenter pilosae, subtus ad venas primarias ferrugineae. Flores axillares solitarii, pedicello 2–2.5 cm. longo. Bracteae exteriores rotundae, 22 mm. longae 18 mm. latae, breviter apiculatae, multinerviae, tenuiter ferrugineae, interiores oblongo-spathulatae, 18 mm. longae, acutae. Hypathium suburceolatum, 6 mm. longum, ferrugineo-tomentosum. Calycis lobi late triangulares, 5 mm. longi, mucronati. Petala staminaque non visa.

Type, *Mexia 8320*, collected along the Río Huallaga above Cayumba, Dept. Huanuco, Peru, alt. 830 meters. *Blakea Mexiae* is related to *B. Spruceana* Cogn. and *B. paludosa* Gl. and is distinguished from both by the barbellate pubescence.

The New York Botanical Garden

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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